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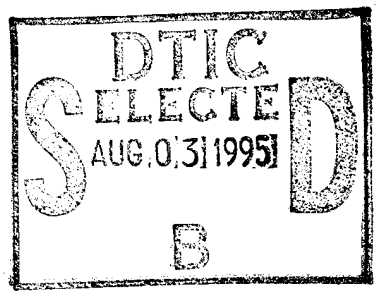
ELF Communications System Ecological Monitoring Program: Pollinating Insect Studies – Final Report

Karen Strickler
J. Mark Scriber



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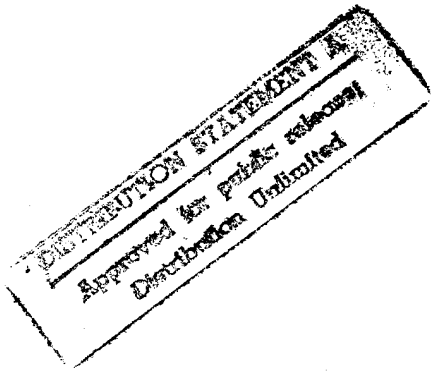

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13. ABSTRACT *(Maximum 200 words)*

The U.S. Navy has completed a program that monitored biota and ecological relationships for possible effects from electromagnetic (EM) fields produced by its Extremely Low Frequency (ELF) Communications System. This report documents the results and conclusions of pollinating insect studies conducted near the Navy's transmitting antenna in Michigan.

From 1982 through 1993 researchers from the Michigan State University (MSU) monitored two abundant species of the genus *Megachile* as representatives of the native bee community. Nine parameters characterizing foraging activity, nest architecture, and mortality aspects were examined in areas near (treatment) and far (control) from the antenna. Foraging behaviors were enumerated and timed by direct observation, while data on nest architecture and mortality were collected using trap-nest techniques. General linear or categorical data models were used to analyze the data.

Statistical analyses indicated significant site-by-year interactions for cell lengths, number of leaves per reproductive cell, and prepupal mortality. Absolute differences were small, inconsistent between species, and inconstant across years. In the case of prepupal mortality, site differences existed during low-power intermittent operation (1986-1988) but not during exposure to a fully operational transmitter (1989-1993). Investigators conclude no adverse electromagnetic effects to pollinating insects.

(ABSTRACT PREPARED BY IIT RESEARCH INSTITUTE)

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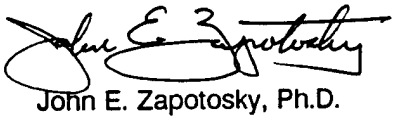
FOREWORD

This report by researchers from Michigan State University (MSU) summarizes the results and conclusions of their study of pollinating insects. In this effort, MSU monitored two species of native bees exposed to electromagnetic fields produced by the U.S. Navy's ELF Communications System in Michigan. The Space and Naval Warfare Systems Command (SPAWAR) funded this MSU study through contracts N00039-81-C-0357, N00039-84-C-0070, N00039-88-C-0065, and N00039-93-C-0001 to IIT Research Institute (IITRI). IITRI, a not-for-profit organization, provided engineering support to MSU and managed their study through subcontract agreements.

MSU initiated their studies in late 1982. Their early efforts focused on selecting study sites, validating assumptions made in proposals, and characterizing critical study aspects. As these tasks were accomplished in 1983 and 1984, MSU then emphasized accumulating a data base through 1993. The MSU research team and IITRI evaluated each study variable for continued funding before contract renewals in 1984, 1988, and 1993. As a result, several originally proposed study elements were either expanded or discontinued in subsequent periods of performance.

Since its inception, scientific peers have reviewed the technical quality of this study on an annual basis. In similar fashion, a draft of this report has been reviewed by peers with experience in entomology, statistics, and electromagnetics. MSU authors have considered, and addressed, peer critiques before submitting their revised manuscript to IITRI. Except for added prefatory and title pages, MSU's manuscript is here issued by IITRI on behalf of SPAWAR without further changes or editing by IITRI or SPAWAR.

Respectfully submitted,
IIT RESEARCH INSTITUTE



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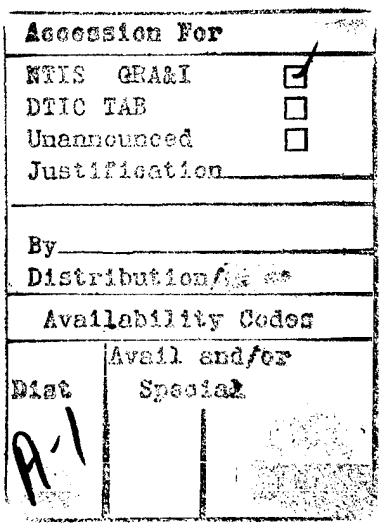

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ELF Communications System Ecological Monitoring Program

BIOLOGICAL STUDIES ON POLLINATING INSECTS: MEGACHILID BEES

Final Report 1994

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GLOSSARY AND LIST OF ACRONYMS

Antenna: 1) Refers to the ELF transmission line, or
2) Used as a fixed effect in statistical models; takes the value "Low" for years before 1989, and "Full" for 1989 and subsequent years.

C5: Camp 5 control site

CATMOD: Categorical data modeling procedure in SAS.

CL: County Line control site

ELF: Extremely Low Frequency

EM: Electromagnetic

Exp: Variable indicating whether the data were from an experimental or a control area.

Exp*Year: Interaction effect of the Exp and year variables in the GLM or CATMOD model.

Expected Sex: The actual or predicted sex of the bee offspring in a cell. Predicted sex is based on the order of the cell in the nest, and the presence of at least one cell of known sex. Females are found in the innermost cells, males in the outermost cells (see p. 16).

F1: Ford 1 (north Ford) experimental site

F2: Ford 2 (south Ford) experimental site

GLM: General Linear Modeling procedure in SAS.

LO: A round leaf piece used to cap a cell or plug a nest. Occasionally an LO is found at the base of a cell or is part of the construction of a cell lining, along with LRs. The bee carries an LO in her mandibles.

LR: An elongate, oblong leaf piece used to line a cell. The bee carries an LR rolled between her legs.

Measurer: variable indicating the person who observed or measured data.

Ow Site: Overwintering site

SAS: Statistical software package (SAS for DOS, 6.04) used in analysis of data.

Season (early vs. late): Nests were classified as "early season" if they were begun on or before the date on which half of the nests of that species were begun during that year. Nests begun on later dates were classified as "late season" nests.

Site [exp]: Site variable nested in experimental areas.

Trip Rank: The number of LO leaves already collected by a bee, including the current LO, in a series of LO trips to cap a cell. Usually the duration of the first 5 such trips are recorded for a given cell cap. These LO trip durations are given Trip Ranks of 1,2,3,4, and 5 respectively.

Yr: Year

I ABSTRACT

High voltage transmission lines and the earth's and other magnetic fields have been shown to affect honeybee reproduction, survival, orientation, and nest structure. ELF EM fields could have similar effects on native megachilid bees.

Two species in the genus *Megachile* were abundant in artificial nests at experimental and control areas in Dickinson and Iron Counties in Michigan. Data on their nest architecture, nest activity, and emergence/mortality were collected between 1983 and 1993. Eight hypotheses concerning the possible effects of ELF EM fields were considered using these data. The ELF antenna has been fully operational since the summer of 1989. Tests of the hypotheses compare control vs. experimental areas before and after the ELF antenna became fully operational.

Our hypotheses involved monitoring changes in cell length, number of cells per nest, length of nest plug, number of leaves per cell, orientation of nest entrances, time to collect a round leaf piece to cap a cell, sex ratio, adult dry weight, and overwintering mortality. We did not detect significant changes in cells per nest, nest plug lengths, nest orientation, time to collect a leaf, sex ratio, or adult weight, that could be attributed to ELF EM fields at experimental areas .

M. relativa cells decreased in length less at experimental areas than at control areas after the antenna became fully operational. Nest orientation for this species changed slightly in one of six localities at experimental areas after the antenna became fully operational.

M. inermis increased leaves per cell slightly at experimental areas relative to control areas. This result is based on greater differences between control and experimental areas during low power years, and no differences during full power years. The proportion of *M. inermis* cells and nests with prepupal mortality increased more at experimental areas than at control areas after the antenna became operational. This result is also based on greater differences between control and experimental areas during low power years, and no differences during full power years. For both of these significant effects, low population numbers at control areas before the antenna was fully operational leave some question as to whether control areas really differed from experimental areas in early years of the study.

These changes may have been caused by ELF EM fields. When change was greater at the control areas, an alternate explanation may be that some unknown factor at the control areas caused the significant change. All of the significant changes were small in magnitude, sporadic, not consistent between species, and do not suggest a pattern of impact on bee populations.

In summary, a few minor changes in bee nesting biology and survival may have occurred due to ELF EM fields. However, these changes are not large enough or consistent enough to raise concerns about the impact of ELF EM fields on Megachilid bees.

II INTRODUCTION

Project Rationale and Overall Objectives.

High voltage transmission lines and fluctuations in the earth's magnetic field have been reported to affect honeybees (Greenberg et al. 1981; Gould 1980). In addition, honeybees have been shown to have an organ in the abdomen consisting of magnetite particles that could be used to detect the earth's magnetic field and thus could be used as a compass in orientation (Gould et al. 1978). This organ appears to be involved in the detection by foraging honeybees of localized magnetic anomalies associated with nectar rewards (Walker and Bitterman, 1989; Kirschvink and Kirschvink, 1991). Honeybees appear to use the earth's magnetic field as a reference system for orientation based on polarized light. The presence of an artificial magnetic field causes a positive deviation in the angle of the waggle dance for bees orienting their dance on a horizontal hive where skylight, but not the sun, is visible (Leucht and Martin, 1990). Because such effects of electric and magnetic fields have been demonstrated, it is possible that ELF EM fields may alter a bee's ability to orient or may otherwise affect its behavior.

Honeybees, however, are rare in the state forest where the Michigan ELF antenna is located, and are unable to overwinter in the harsh climate of Michigan's Upper Peninsula (Fischer, 1983 Annual Report). Therefore, native bees are a better choice for ecological studies of the resident bee fauna. Native bees are particularly important in ecological communities such as those in the vicinity of the ELF antenna because they are pollinators of flowering plants, and are therefore important to the reproductive success of these plants.

With the exception of bumblebees and some halictids, native bees are solitary, meaning that each female constructs and provisions her own nest rather than having a special queen caste responsible for reproduction. Solitary bees have several advantages for ecological studies. As "mass provisioners", they create a discrete cell for each offspring, and fill it with a provision mass of pollen and nectar prior to laying the egg. The bee does not add more provisions after the egg is laid. A series of such cells, each with a provision mass and egg, are created in succession by each female. The provisions that go into each cell are a direct measure of parental investment in an offspring (Strickler 1979; Cowan 1981; Johnson 1983; Danforth 1990). The size

of the adult bee that emerges from each cell is correlated with the amount of provisions provided to it, and with the size of the cell in which the larva develops (Krombein 1967; Klostermeyer et al. 1973; Trivers and Hare 1976; Alcock 1979; Torchio and Tepedino 1980; Johnson 1983; Danforth 1990). However, there is a tradeoff between the investment per offspring and the rate at which offspring are produced. The more the bee invests per offspring (ie, the larger the offspring), the fewer offspring she will produce. If bees are disoriented, agitated, or slower at foraging, they may invest less per offspring, produce fewer offspring per unit time, or both. Solitary bees are unusual in having this direct relationship between parental investment per offspring, adult size, and reproductive output.

The nesting biology of some species of solitary bees in the family Megachilidae is especially easy to study because they accept artificial nests placed in the field. These bees typically nest in abandoned beetle bores in dead logs. "Trap nests" of drilled blocks of wood are also used by bees as nest sites. Such artificial nests can be placed in habitats where bees are expected to nest, in order to increase the sample of nests available for study, and to standardize such characteristics of the nest as bore depth and diameter (Krombein, 1967). Trap nests are used in the management of the Alfalfa Leafcutting Bee, *Megachile rotundata*, for pollination of alfalfa (Stephen, 1962, 1981; Bohart and Knowlton, 1964; Johansen et al., 1969; Bohart, 1972; Gerber and Klostermeyer, 1972; Hobbs, 1972; Baird and Bitner, 1991), and the Blue Orchard Bee, *Osmia lignaria* for the pollination of fruit trees (Torchio 1981a,b; 1982a,b,c; 1984a,b; 1985). Thus there is an extensive literature on megachilid biology.

Although the effects of electromagnetic fields on solitary bees had not been studied previous to the ELF project, research on the effects of high tension wires and other magnetic fields on honeybees suggested working hypotheses on which to base our analyses of megachilid nesting biology. Of possible relevance to megachilid behavior are an alleged greater tendency for dispersal, and greater levels of activity (Wellenstein, 1973), as well as reduced reproductive output, lower overwintering survival, and modifications of nest structure (Greenberg et al., 1981) when colonies were exposed to electromagnetic fields from high voltage transmission lines. Disturbance of colonies under transmission lines can be attributed to electric shock from induced hive currents, especially under wet conditions (Bindokas et al., 1988). Although induced currents are less likely in trap nests than in honeybee hives, the possibility of stress or disturbance from electromagnetic fields should be appraised. In addition, disorientation due to fluctuations in ELF magnetic fields is possible if megachilids share the honeybee's ability to detect magnetic

fields. (Gould et al., 1978, 1980; Gould 1980; Tomlinson et al. 1981; Walker and Bitterman, 1989; Kirschvink and Kirschvink, 1991). No data exist on the ability of megachilids to detect magnetic fields.

Nesting Biology of Megachilid Bees

A decision to restrict our study to two species of leaf-cutting bees, *Megachile (Megachile) relativa* Cresson and *Megachile (Megachile) inermis* Provancher, was made in the fall of 1986 (1986 Annual Report). *M. inermis* and *M. relativa* have similar nest architecture in that both line their cells with pieces of cut leaves. However, the two species differ in size, and may therefore partition their time and the space in their nests differently. Aspects of the biology of both species have been described generally for populations in Wisconsin and Canada (Medler, 1958; Medler and Koerber, 1958; Stephen, 1955,1956; Longair, 1981).

The general structure of the nests of the two species is depicted in Fig. 1. The bee may leave some space at the base of the nest (the basal space) unoccupied by cells for offspring. She may then cut and bring to the nest a few round pieces of leaf that are added one at a time to form the base of the first cell. Next she cuts and brings to the nest several elongate pieces of leaf (LRs) in succession. These are used to line a tube- or cup-shaped cell that is slightly longer than her body. Next she makes a series of pollen and nectar foraging trips to fill the cell with the discrete provision mass that will be the larva's food supply. When provisioning is complete, the female lays an egg. Fertilized eggs become females while unfertilized eggs become males. The female has voluntary control over fertilization and thus the sex of the offspring in each cell (Klostermeyer and Gerber, 1970). After laying the egg, she cuts more leaves, this time round in shape (LOs), to cap the cell. Sometimes she adds chewed leaves, dirt, or bits of wood to separate the cells. Next she cuts more elongate leaves for the second cell, and repeats the process. Thus a linear series of cells is constructed in the nest bore. Typically, the cells at the base of the nest are more likely to contain females and the cells near the entrance are more likely to contain males (Krombein, 1967). Since females are usually larger than males in these bees, cells at the base of the nest tend to be larger than cells near the entrance. When she has completed the last cell of the nest, she constructs a series of plugs of round leaves, chewed leaves, dirt, chewed wood, and possibly other material. *M. relativa* frequently includes empty "vestibular" spaces between segments of plug. *M. inermis* and some *M. relativa* create one long mass of plug material after completing the repro-

ductive cells. In nests of both species there is usually a space between the outermost plug and the opening of the nest, called an "indentation".

Each female may construct several such nests over her life time. The adult life span is no more than one season; adults do not overwinter. Some nests are abandoned before they are finished because the bee has died, or for other unknown reasons. Some incomplete nests may be usurped by other species of wasps and bees, which construct their own nests in the unused space of the trapnest.

Inside each cell the egg hatches, and the young larva feeds on the provisions prepared by its mother. Both *Megachile* species at our sites are univoltine (with a few exceptions; see Emergence Results), and both overwinter as prepupae. Pupation occurs in spring, and adults emerge soon after, in June and July at our study sites. A variety of parasites may emerge from the cell instead of the original bee. Oviposition by parasites of the genus *Coelioxys* (Megachilidae) often occurs while the cell is being provisioned, when the mother host bee is out of the nest on a pollen foraging trip, or on a round-leaf foraging trip just after laying her egg. Other parasites may lay their eggs in empty nests holes (*Anthrax* spp., Diptera: Bombyliidae) or in complete nests (chalcids; Hymenoptera: Chalcidoidae).

Hypotheses Tested

During the first four years of the project, 1983-1986, data on nest architecture, nest orientation, emergence/ mortality and nest activity were collected. Based on these data, six tentative hypotheses concerning the effects of ELF EM fields on *Megachile* behavior were specified in the 1986 Annual Report. The initial hypotheses were modified in subsequent reports based on our ability to gather sufficient sample sizes to detect differences between experimental and control areas. The hypotheses are expressed in the following sections as null hypotheses, ie., hypotheses of no difference between experimental and control areas, that we will try to disprove statistically. The "Rationale" sections explain the possible effects of ELF EM fields that may cause a rejection of the null hypothesis.

Hypotheses Involving Nest Architecture

Hypothesis 1: The average length of cells for each offspring, and/or the average number of cells produced per nest is unchanged by exposure to ELF electromagnetic fields.

Rationale

Honeybee reproductive output decreased on exposure to high voltage transmission lines. Capped brood, which normally averaged 12,000 per hive, decreased to as low as no brood after 8 weeks of exposure (Greenberg, et al., 1981). ELF EM fields may have a similar effect on the number of cells produced by megachilids. Furthermore, ELF electromagnetic fields may affect cell size and nest architecture in various ways. For example, if bees are disoriented by the fields, they may gather resources (leaves, pollen) more slowly when exposed to the fields than when not exposed. As a result, they may produce new cells at a slower rate, or they may produce smaller cells.

Previous studies have found that the weight of offspring of the generalist megachilids, *Osmia lignaria* and *O. cornifrons*, is lower if their cells were produced late in the season rather than early in the season (Torchio and Tepedino, 1980; Sugiura and Maeta, 1989). These species also showed an increase in the proportion of male offspring (the smaller sex) produced late in the season. A reduction in offspring size late in the season is related to reduced foraging rates due to aging of the bee (Torchio and Tepedino, 1980, Tepedino and Torchio, 1982; Sugiura and Maeta, 1989). Similarly, ELF EM fields may slow the foraging of *M. relativa* and *M. inermis*, resulting in smaller bees produced in smaller cells. A size reduction could affect cells with offspring of both sexes, or it could reflect the production of a greater proportion of male offspring, since males are the smaller sex in both *Megachile* species. An additional complication is that female size decreases more than male size late in the season (Torchio and Tepedino, 1980). Thus we might expect female cells to be affected more than male cells by stresses from ELF EM fields.

In contrast to the generalist megachilids, the pollen specialist *Hoplitis anthocopoides* did not show a reduction in offspring weight late in the season, in spite of reduced foraging rates (Strickler, 1982). Rather, it was hypothesized that slower foraging rates led to fewer offspring per nest late in the season as compared with early in the season for this species. Similarly, *M. relativa* and *M. inermis* may produce fewer cells per nest in response to slow foraging rates due to ELF EM fields.

In testing hypothesis 1 we are interested in determining whether there are differences between experimental and control areas in cell lengths and number of cells per nest. Ideally, one hopes to find no differences between experimental and control areas, and between years, prior to the ELF antenna becoming operational. Then, if significant differences between experimental and control areas appear after the antenna is functioning at full power, we can attribute these differences to ELF EM fields.

Hypothesis 2: **Bees exposed to ELF EM fields, and bees not exposed, will make nest plugs of the same thickness.**

Rationale

Abnormal deposits of up to 48g of propolis were present at honeybee hive entrances under high voltage transmission lines, presumably in response to stress connected with electric fields at the nest entrance (Greenberg et al, 1981). This suggests the possibility that megachilid bees will respond to disturbance from ELF EM fields by increasing the amount of nest "padding". This may be reflected in larger cells (tested in hypothesis 1) and/or increased nest plug length.

Hypothesis 3: **The number of leaves used to line a cell is unchanged when bees are exposed to ELF EM fields.**

Rationale

Bees may pad a cell with extra leaves as a result of stress due to electromagnetic fields, just as they may pad a nest with plug material. We can easily determine the number of elongate leaves used to line a cell by taking the cell apart after bee emergence and counting leaves.

Hypothesis 4: **The relative acceptability of nests oriented in a NS direction vs. nests oriented in an EW direction does not change when bees are exposed to ELF EM fields.**

Rationale

Honeybees may use the earth's magnetic field under special circumstances to orient their comb (reviewed in Gould, 1980). The fluctuating ELF magnetic fields could disturb any biases that megachilids normally have for

nest orientation, or could cause greater acceptance of nests oriented in certain directions in order to reduce disturbance by the fields.

Hypotheses Involving Nest Activity

Hypothesis 5: The duration of round leaf (LO) foraging trips remains the same when bees are exposed to ELF EM fields.

Rationale

Honeybee activity, measured by honey production, allegedly doubled under high voltage electromagnetic fields in one study (Wellenstein, 1973). In contrast, colony weight, a measure of rate of honey accumulation and brood production, decreased by as much as half for colonies exposed to high voltage transmission lines in a different study (Greenberg et al., 1981). In a third study, there were dose-related lags in colony weight gain, with the maximum difference being a doubling of exposed hive weights compared with more than a six fold increase in control colonies in 5 weeks (Greenberg et al., 1981). Foraging rates were decreased by as much as half in exposed colonies in this study (Greenberg et al., 1981). Honeybees also had an increased tendency to sting under high voltage transmission lines (Wellenstein, 1973). ELF EM fields might similarly affect megachilid bee activity by disorienting or agitating the bees so that the duration of leaf- and pollen-foraging trips is altered. Interference with magnetoreception might play a role in disorientation. Changes in electric potential of the bees, or of the plants on which they forage (Erickson, 1975; Erickson and Buchmann, 1983), or changes in the electric potential of antennal chemosensilla that detect plant odors (Erickson, 1982) might also affect the bees' foraging rate.

Leaf-foraging trips for *M. inermis* are easy to recognize behaviors, usually lasting less than a minute in duration. Many of these trips are taken in succession, so within and between bee variability can be analyzed, and a potentially large sample of leaf collecting trips can be timed. In the 1986 Annual Report we demonstrated that the collection of LO leaves was the most consistent behavior of the leaf-cutting bees under study. We argued that this is probably because it is adaptive to close the cell as quickly as possible after the egg is laid to avoid parasitism. Thus, our analysis focuses on LO trip durations.

Hypotheses Involving Emergence:

Hypothesis 6: The relative proportions of emerging males and females is unchanged by exposure to ELF EM fields.

Rationale

We have argued (p.7) that changes in sex ratio could occur as a result of stress from ELF EM fields. In particular, if foraging rates increase due to disorientation from ELF EM fields, bees may increase the relative number of male offspring that they produce. This is because males are the smaller sex, requiring less parental investment. It is appropriate, therefore, to consider whether there are any significant changes in the relative proportions of emerging males and females that can be attributed to ELF EM fields.

Hypothesis 7: Newly emerged bees exposed to ELF EM fields are the same weight as newly emerged bees not exposed to ELF EM fields.

Rationale

In testing for effects of ELF EM fields on body size, we are testing for effects on the amount of provisions per cell supplied by the mother bee. Weight depends directly on the amount of provisions in the cell (see p. 3). If ELF EM fields have a major impact on bee foraging behavior, the results for hypotheses 1, 6, and 7 should be consistent. Smaller cells, smaller bees, and more males might be expected.

Adult weight may be a more appropriate measure of parental investment per offspring than is cell length. Provisioning a cell typically takes much more time than constructing a cell. A larger cell with more leaves may have less provisions and thus yield a smaller offspring than a smaller cell with more provisions, which cost more in time and energy to gather than leaves. Adult weights might also decrease due to a reduction in assimilation efficiency of the feeding larva. This might occur independent of changes in cell length and sex ratio.

Hypothesis 8: Overwintering mortality of megachilid bees is unchanged by exposure to ELF EM fields.

Rationale

Overwintering mortality of honeybee colonies under high voltage transmission lines increased from 29% when hives were shielded to 71% when they were fully exposed to electrical fields (Greenberg et al., 1981). We would like to test for a similar effect in megachilid bees. To do this requires comparing control and experimental areas in the proportion of cells that suffer mortality during the prepupal (overwintering) stage, relative to the number of cells that survive to the prepupal stage or beyond (pupa and adult) (see results section for further discussion).

Ideally one hopes to find no differences in overwintering mortality between experimental and control areas prior to the ELF antenna becoming operational. Then if significant increases in overwintering mortality between experimental and control areas develop after the antenna is functioning at full power, we can attribute these differences to ELF EM fields.

III METHODS

Data on nest architecture and nest orientation were obtained by placing trap nests in the environment, and allowing bees to construct nests in their choice of traps during the summer. The following spring, various parameters of their nest architecture were measured. Bee and parasite emergence and larval and pupal mortality were also recorded in the spring. Data on nest activity data were gathered during the summer season while the bees constructed their nests.

The methods discussed below compares, where appropriate, changes in protocol over the years, especially pre- and post-1987. Where no such comparisons were made, no significant changes in protocol were made.

Trap Nesting Methodology

Bees were provided with fresh trap nests each year. Trap nests consist of elongate white pine pieces 19x19x153 mm. Most of these nests were drilled lengthwise to a depth of 142mm. Exceptions were the largest diameter nests pre-1987, and half of the 1987 large diameter nests. These nests were drilled to only 107mm.

Prior to 1987, drill bits with seven different diameters were used to create trap nests (Table 1). The maximum diameter was limited by the dimensions of the trap nest, and by availability of long drill bits.

In 1987 only the 5.5mm bit and the 11.0mm bit were used because these diameters were accepted most often in 1985 by the two *Megachile* species under study (see 1986 annual report). In 1988-1991 small nests were made with both 5.5 and 6.0mm drill bits because analysis of 1986 nests indicated that the 6.0 mm diameters were common, and because it was feared that 5.5 mm diameters would skew the sex ratio in favor of male offspring and thus bias the cells towards shorter lengths. Bore diameter has been shown to influence sex ratio for other trap nesting species (Stephen and Osgood, 1965; Krombein, 1967; Cowan, 1981; Tepedino and Torchio, 1989).

Prior to 1987, twelve nests, two of each bore diameter, were bound together with plastic strapping into a "block", so that one of each bore diameter faced each direction, and no two bore entrances were adjoining (Fig. 2a). Starting in 1987, two 11.0mm bores and four 5.5mm bores were arranged

randomly in each direction (Fig. 2b). In 1988-1992, three of the small nests were 5.5mm and one was 6.0mm in each direction. We did not realize that the 1987 random arrangement of nest entrances differed from the 1983-86 pattern of no adjoining entrances until blocks for 1987 had already been prepared. We observed no obvious changes in bee behavior at the hutches as a result of this change in nest entrance arrangement, although we made no systematic effort to compare the two arrangements.

"Hutches" consisting of a wooden frame with four shelves and a roof were used to hold the blocks of trap nests (Fig. 3). Four blocks of nests were placed randomly on each shelf, making a total of 192 nests present at any one time. The hutch was open on both sides, so half of the nests opened in each direction. The shelves were roughly 0.1, 0.4, 0.8, and 1.1 meters from the ground.

Four study sites were selected by 1984 for placement of hutches (Fig. 4). Two are experimental sites along the ELF antenna: Ford 1 and Ford 2 (F1 and F2), and two are control sites: Camp 5 and County Line (C5 and CL). The study sites are described in the section titled "Description of Sites", p. 20. Further information can be found in the 1985 annual report. Three sets of two hutches, making a total of six hutches, were placed at each of the four study sites. In each set of two hutches, one hutch was oriented in a north-south direction so that its nests open to the east or west, and one hutch was oriented in an east-west direction so that its nests open to the north or south. The two hutches in each set were placed near each other in edge habitats between open areas where there are abundant flowering plants, and woods where natural nest sites are available. In 1983, only the F1 site had been chosen for study in the spring. The CL and F2 sites were added in mid-season. Generally, only one or two sets of hutches were in place that year.

When a nest was occupied by a megachilid bee, it was given a number that included site (C5, CL, F1, or F2), hutch direction (NS or EW), nest entrance orientation (E, W, N, or S) and shelf height (1-4, top to bottom). This number was written on the side of the nest. Position on the shelf and in the block of nests was not recorded.

Once a nest in progress was identified, the depth of empty tunnel space was recorded daily (pre-1987) or every 2-7 days (1987-92). This information, coupled with nest architecture measurements taken the following spring, allowed us to estimate which cell the bee was constructing on the day the nest was first located. Assuming that the bee takes approximately one day to complete a cell, we estimated the dates on which the nest was begun

and finished. Nests were classified as "early season" if they were begun on or before the date on which half of the nests of that species (pooled over all sites) were begun during that year. Nests begun on later dates were classified as "late season" nests. When the nest was completed, it was removed from the block, and replaced with an empty nest of the same bore size.

Each completed nest was stored in a large centrifuge tube with cloth covering the opening. Tubes were placed in wooden overwintering boxes built to fit the hutch shelves. Prior to 1987, completed nests were brought to Channing, MI to overwinter, in order to avoid vandalism and marauding animals. However, starting in 1987, nests were left in overwintering boxes at the site where they were constructed. Overwintering boxes were not left on hutch shelves as in the past, but rather were elevated about a foot off of the ground and camouflaged with branches, bark, and leaves in order to avoid vandalism. Fortunately, overwintering boxes were not vandalized at any of the sites, although hutches were damaged and occasionally disappeared during the winter.

Beginning with nests constructed in 1990 and continuing in 1991, a manipulative experiment was initiated to compare overwintering mortality of nests constructed at one site but overwintered either at an experimental or a control site. The results of this experiment cannot determine unambiguously whether ELF EM fields affect overwintering mortality, because no manipulations were done before the antenna was operational. However, the experiment may offer further evidence in conjunction with broader comparisons between sites and years. For the manipulative experiment, each year one third of the nests constructed at the F2 experimental site were moved to the C5 control site in mid-September for overwintering. The nests that were moved were chosen to represent hutches and dates of nest initiation in the same proportions as the nests that remained at the F2 site. The number of F2 nests overwintering at C5 approximately equaled the number of C5 nests overwintering at C5. Nests from both sites were placed in overwintering boxes in the same directions as they were constructed, but C5 and F2 nests were mixed and positioned randomly with respect to bottom vs. top, right vs. left side of the overwintering boxes. The reciprocal experiment, overwintering C5 nests at F2, could not be conducted because there were insufficient C5 nests. Nest numbers were considerably reduced at all sites in 1992, so the experiment was discontinued.

Nest Architecture Measurements

Nests constructed by *M. relativa* during 1983 were measured in the spring of 1984 prior to emergence. Nests constructed by *M. relativa* during 1985 were measured after bee emergence, in November and December, 1986. Nests constructed during 1985 by *M. inermis* were measured after emergence in August, 1987. Most 1986 *M. relativa* nests were measured before emergence in 1987, so that we would know with certainty the species and sex of the occupant of each cell. The 1986 *M. inermis* began to emerge in spring 1987 before we began measuring their nests, so most *M. inermis* nests were measured after bee emergence. The 1987-91 nests were measured sufficiently early in May of 1988 - 1992 that we were able to complete nest measurements of both species before they emerged in June and July.

Measurements for 1986-1990 nests were made at our Crystal Falls, MI lab. However, we learned in 1989 that 60Hz EM fields are relatively high in Crystal Falls due to the presence of numerous power lines. In the laboratory, electric lights and wiring in the walls also created relatively high EM fields (ELF Communications System Ecological Monitoring Program: Electromagnetic Field Measurements and Engineering Support - 1990). Therefore beginning in 1989, unopened nests and rearing tubes were kept at a holding site constructed by the ELF Small Mammal and Bird Project in woods 5 miles south of Crystal Falls. Nests were brought to the Crystal Falls lab only briefly for measurement. There they spent up to 6 hours outside the house where 60 Hz fields were low, and no more than 2 hours in the lab for measurements. In addition, in 1990 and 1991, measurements were made in wire mesh Faraday cages constructed by IITRI to minimize exposure of developing bees to electric fields (Fig. 5). Just before and just after measurements, nests and cells were stored in another Faraday cage on the front porch of the Crystal Falls Lab (Fig. 6). In 1992 we moved our research to a smaller house in Crystal Falls because fewer assistants were required. Unfortunately, EM fields were considerably higher in this new house, so all nest architecture measurements were made at the holding site in 1992 and 1993 (nests constructed in 1991 and 1992).

After recording nest number and bore diameter, nests were split open lengthwise with a chisel. Total bore depth, non-reproductive spaces (basal space, vestibular spaces, associated caps, nest plugs, and indentation) were measured with the cells intact. Each cell was then removed and measured from the base of the cell to the position of the outermost leaf in the cell cap

(Fig. 7). Cell lengths measured after emergence are likely to be somewhat more variable than cell lengths measured before cell emergence, because emergence damages the cell cap. In such cases it is sometimes difficult to determine where the edge of the cell cap starts.

The nest number that is written on each nest includes information on the site where the nest was created, so nest architecture measurements of pre-1988 nests were not blind to site. However, our measurements of the 1988 - 1991 nests were made blind to site in the following manner. Before nest measurements were made, students who did not measure nests spent a day crossing out nest numbers and replacing them with a random number independent of site. A data base not available to the nest measurers recorded the original nest number, and the random code number assigned to it. Nests were then measured without knowing at which site they were constructed. After all measurements were complete, the random number was associated with its original nest number, including site.

Since more than one person measured nests, we attempted to divide the nests equally by site and date of nest initiation among all measurers. Thus individual biases in measurement are distributed evenly between sites and dates.

Emergence Data

Nests created in 1985 were checked daily in the spring of 1986 for bees that had emerged from the nest and were in the centrifuge tubes. In subsequent years, after taking nest measurement in the spring, cells from which nothing had yet emerged were placed in individual plastic culture tubes or 2 oz. transparent plastic "Solo" rearing dishes, and labeled with nest and cell identification numbers. In 1987 and 1988 tubes were kept in the Crystal Falls Laboratory at room temperature (approx. 68°F) until emergence. Beginning in 1989, cells in rearing dishes and culture tubes were returned to the holding site in woods 5 miles south of Crystal Falls after nest measurements were complete. Cells were checked daily for emergence. In all years, date of emergence, species, and sex of offspring were recorded. Emergence took longer in years when cells were outside at the holding site than when cells were in the lab, because of cool spring temperatures at the holding site. However, this should not have affected overwintering mortality or sex ratio, two variables of interest. Adult weight may have been affected, but equally over all sites.

Some bees were saved for dry weight measurements (see below) and identification. Bees were identified by G. Dahlem, V. Scott, and K. Strickler based on Mitchell (1962), and by comparison with reference specimens provided by T. Griswold, ARS Bee Laboratory, Utah State University, Logan Utah.

The remaining adult bees were released at the sites where their nest had been constructed the previous summer. The Faraday cages mentioned above were intended to insure that released bees were not affected by 60 Hz electric fields when nest architecture measurements were taken. Effects of 60 Hz fields might be mistaken for (or might mask) effects of the ELF antenna's 76 Hz fields, and affected bees might alter the genetic makeup of natural populations. Parasites were collected and not released. Also, F2 nests that had overwintered at C5 were not released at the research sites.

Cells that showed no signs of emergence were opened in August (1986-92 nests), or when the nest was measured (1985 nests). Contents were recorded to indicate at what stage mortality had occurred.

Offspring sex, expected sex of a cell, and sex ratio. Our analyses indicate that the offspring's sex contributes significantly to variance in cell length and leaves per cell. However, the sex of the offspring is known only for a small proportion of the cells, since many offspring die in the larval and prepupal stages, and these cannot be sexed. Furthermore, parasites emerge from some cells rather than *M. inermis* or *M. relativa* individuals. In an attempt to increase our sample size, we created a new variable in our data set that indicates the expected sex of a cell. We can predict the expected sex for many of the cells that did not have a *Megachile* emerge. Emergence data for 1987-1992 nests (and for other trap nesting wasps and bees: Krombein 1967; Cowan 1981; Sugiura and Maeta 1989) indicates that when a nest contains females, they are almost always in inner cells relative to cells containing males. Exceptions are thought to be failures of fertilization, diploid males, or usurped nests (R. Owen, personal communication). In our study, very few males emerged from cells that were deeper than a female cell: only 4 of 629 *M. relativa* and 7 of 1011 *M. inermis* in 1987, one of 621 *M. relativa* and 9 of 1969 *M. inermis* in 1990, and one of 452 *M. relativa* and 3 of 2160 *M. inermis* in 1991. None of the *Megachile* emerging in 1988, 1989, or 1992 (a total of 1082 *M. relativa* and 2938 *M. inermis*) deviated from the typical pattern. Therefore, cells of unknown sex deeper in the nest than a cell with a female offspring can be assumed to be female. Conversely, cells with unknown sex that follow a male cell can be assumed to be males. (It is possible, though improbable in

our opinion, that most larval mortality affects *Megachile* in the "wrong" position, so that our predicted sex is incorrect for a significant number of cells.)

The expected sex of a cell is the predicted sex of the cell when sex can be deduced, or the actual sex when sex is known. In statistical analyses where female and male cells are treated separately, expected sex increases the number of cells that can be included in the analysis by 2.6 fold for 1985 *M. relativa*, by 2.4 fold for 1985 *M. inermis*, and by 1.2-1.8 fold for both species in subsequent years.

Expected sex of a cell is a useful variable in analyses of cell length and leaves per cell. However, it is not a good variable to use in estimates of sex ratio of the population. This is because expected sex cannot be deduced in nests that have only a single dead cell, or in nests that have no emergence in the innermost cell and only males in subsequent cells. Since the innermost cell has the highest proportion of female offspring, using expected sex of a cell to estimate sex ratio will bias the sex ratio toward males. Instead, we use the ratio of male to female adult and pupal offspring that could be sexed with certainty.

Offspring Weights. Two or three bees (typically one female and one - two males) from each 1987 - 1991 nest were collected for dry weight measurements and for confirmation of species identification. Bees were collected within hours of emergence without being released, so their crops were empty. All individuals defecated as prepupae, and none defecated again until after release. Thus much of the variability in weights that would be expected from a sample of field collected bees was eliminated. Dry weights were obtained by drying bees in a desiccator over P_2O_5 to constant weight. Constant weight was defined as two weights taken 48 hours apart that were within 0.5mg of each other. The lower of these weights was used in analyses.

Leaf Counts

The number of elongate leaves that were used to construct a cell was determined for 1985-1992 *M. inermis* cells and 1986-1991 *M. relativa* cells that were still in good condition once emergence was complete. Leaves lining *M. inermis* cells overlapped, but were easy to tease apart and count. Leaves lining *M. relativa* cells were smaller, and were fastened together so that a microscope was often needed to determine where one leaf ended and the next began. When in doubt, leaf counts for *M. relativa* cells were not recorded.

Data Entry for Nest Architecture, Emergence, and Leaf Count Data

Nest architecture measurements, emergence records, and leaf counts were recorded manually in the spring and summer on data sheets for each nest. Dry weights were added during the following fall and winter. Nest architecture data were typed into an R-Base database management file on a 486 33MHz PC computer. Relevant subsets of the data were transferred from R-Base to SAS data files for statistical analysis with SAS for DOS 6.04.

Nest Activity

One or more observers gathered data on behavior of individual bees at the nest every year between 1983 and 1991. In the 1986 Annual Report, we decided to focus on the collection of round pieces of leaf (LO trips) used in capping a cell. Analysis (1986 Annual Report, p. 20-21) suggested that this was the most consistent of the three main behaviors in nest construction (collection of pollen, collection of elongate leaves for cell lining, and collection of round leaves for cell caps). LO trips probably involve fewer extraneous behaviors such as sunning or taking nectar than do pollen or elongate leaf collecting trips. Thus residuals for the transformed duration of LO trips could be normalized for statistical analysis. Consistency in LO trip durations probably results from the necessity to cap the cell rapidly to avoid parasitism after laying an egg.

Prior to 1987 each observer watched a single bee for several days in succession, until the nest was complete. This protocol generated a great deal of information on the variability in behavior within a bee, but less information on between-bee variability. Also, few bees were timed at the control sites. In 1987 - 1991 field seasons we maximized the number of bees timed per day, rather than timing one bee for long periods of time. Observers became adept at locating a bee that was about to lay her egg, and were able to focus on timing the first few LO trips that the bee made after laying her egg. Generally, we timed 3 such trips in succession before searching for another bee that was about to collect LO leaves. Only the first three trips are included in statistical analysis, because this minimizes the variability in the duration of a given bee's cell capping trips. Our 1987 analysis suggested that the number of LO trips that the bee made since an egg was laid is important, because LO

trips tend to increase in duration with each successive trip after egg laying (1987 Annual Report). In 1987 we did not keep track of this "trip rank" number but during the 1988-1991 field seasons we attempted to record this number when timings were made. Only LO durations for which the trip rank order was known are used in the analysis.

During the 1987 - 1991 field seasons, four observers were rotated between sites every 3 to 4 days, so that biases between observers would be distributed evenly between sites and dates. On a given day, two observers visited a control site and two an experimental site.

Prior to 1987, the duration of LO trips was determined by using a watch to record the hour, minute, and second that the bee left the nest and returned to the nest. Starting in 1987, we used portable Tandy 102 computers that were programmed as event recorders. When the program was activated, the observer was prompted for information on the nest number and site, and some weather data (see below). The program automatically numbered the observed activities in sequence. Hitting the space bar recorded the time to the nearest second at which the bee left the nest or returned to the nest. A single letter code indicated what cargo (e.g., LOs), if any, the bee brought back to her nest. An editing feature allowed the observer to correct errors made during the timings, or to delete times that resulted from hitting the space bar inappropriately. Data were down-loaded to a Zenith personal computer at our field headquarters, and later transferred to an INGRES data base file on the VAX computer in the Department of Entomology at MSU. Duration of each trip was calculated in INGRES by subtracting the time when the bee left the nest from the time when the bee returned. More recently, activity data were transferred to RBase on our 486 computer. Relevant subsets of the data were used to create SAS data files for statistical analysis.

Weather Data

Data on long-term trends in temperature and precipitation were obtained from the ELF Herbaceous Plant Cover and Tree Studies project, based at Michigan Technological University (MTU). Dr. Hal Liechty of the MTU project kindly provided us with an ASCII file of daily summaries of average, 3 hr. minimum, and 3 hr. maximum air temperatures, and total daily precipitation. He monitored ambient air temperature and precipitation (among other variables not of interest to us) at MTU's Red Pine Plantation sites: a

treatment site under the ELF antenna, 10 miles North of our F1 site; and a control site 9 miles south of Crystal Falls. Despite the distance between the MTU sites and the sites that we used in the Native Bee ELF project, major climatic trends and differences between years in temperature and precipitation were representative for the region. Climatic trends should affect floral resources and thus bee population size, cells per nest, offspring weight, and percent mortality. For further information on the MTU ambient monitoring system, see Appendix B of the 1985 Herbaceous Plant Growth and Tree Studies Project Annual Report.

Description of sites

Figure 4 shows the location of the study sites relative to the ELF antenna. Three sites were located on Copper County State Forest Property in Dickinson Co. in the Upper Peninsula of Michigan. A fourth site (C5) was located in Iron Co. on property leased by the Michigan Department of Natural Resources to Champion Paper Company. Permission to use these sites is gratefully acknowledged.

The C5 site was located 6.7 km south of Route 69 and about 0.8 km west of Camp 5 road in Iron County, Michigan (Township 42N, Range 31W, Section 14). The area had recently been logged, and nearby forests continued to be logged within about one km of our hutches during the experiment. An abandoned railroad bed ran north to south through the site. Camp 5 creek ran through the site, creating a cut-over swamp and flood plain (fig. 8). Two hutches were located at the south edge of this flood plain, and two hutches were located in an open depression next to the abandoned railroad bed. Until mid July 1990 the last two hutches were at the north edge of the flood plain, north of C5 creek. This site was not close to *Cirsium palustre* populations, and attracted few *M. inermis*.

In spring, 1990 a beaver made a dam across C5 creek, making access to the north hutches impossible by crossing the creek next to the railroad right-of-way. For several months we walked around the edge of the flood plain to reach the north hutches. However, as the water behind the dam increased, the flood plain turned into a shallow lake. On July 25, when water was within 10 feet of the north hutches, we moved them to the south side of C5 creek. The hutches were relocated to an elevated site about 20 feet west of the railroad right-of-way, near a large patch of *Cirsium palustre*. The bee population that uses nests at these hutches should have been the same as in

the original location. However, being closer to flower populations, more bees nested at the new location.

Nearby woods consisted primarily of *Populus tremuloides*, with occasional *Larix decidua, Picea glauca,* and *Prunus serotina.* Shrubs in the vicinity included *Alnus rugosa, Vaccinium* sp., *Salix* sp., *Spirea alba,* and *Rubus alleghe-niensis.* Herbaceous plants included *Cirsium palustre, Fragaria virginiana, Hier-acium* spp., *Trifolium* spp., and *Solidago* spp.

The CL site was located about 1.7 km north of Route 69 on the east side of County Line Road, in Dickinson Co., (Township 43N, Range 30W, Section 19). Logging continued within a km or so of the hutches during the experiment. This site had very sandy soil and was the driest of our sites. Hutches were located at the edge of clearings in *Populus tremuloides* woods, with occasional *Acer saccharum, Betula papyrifera, Abies balsamea,* and *Pinus resinosa.* Two hutches were adjacent to a patch of trees north of a logging road through the sandy clearing. Two were east, and two west of a marshy, low lying area south of the logging road (fig. 9). *Hieracium aurantiacum* carpeted the ground at this site in June, when rain was sufficient. Bracken fern was common near the east hutches which were in a shadier location than the others. Other flowering plants that were common in the area include *Cornus canadensis, Campanula rotundifolia, Fragaria virginiana, Rubus spp., Solidago spp., Vaccinium spp., and Prunus pensylvanica.* Small patches of *Cirsium palustre* grew in the marshy area south of the logging road. *Epilobium angustifolium* was abundant at this site in 1983, but decreased rapidly thereafter. Only a couple of stems were present in 1987, and none in subsequent years.

The F1 site was located south of Turner Road, and north of the Ford river, 20 km east of Channing. (Township 43N, Range 29W, Section 14). The hutches were located at the edge of a flood plain, bordered on the north by a Red Pine plantation, and the south by vegetation along the river consisting of *Populus balsamifera, Populus tremuloides, Fraxinus nigra,* and *Alnus rugosa.* A corridor had been cut through the pine plantation for the ELF antenna, which runs NE-SW through the site. Two hutches were east of the antenna, at the north edge of the flood plain. Two were a similar distance west of the antenna. Two were in a shady clearing further west of the antenna at the northwest edge of the flood plain (fig 10). Flowering plants near the hutches included several species of *Cirsium,* especially *C. palustre* and *C. arvense, Ur-tica dioica, Solidago* spp., *Hieracium* spp., *Hypericum perforatum, Aster* spp., *Rubus* spp., *Humulus lupulus, Linaria vulgaris,* and *Vaccinium* spp.

The F2 site was located about 0.8 km south of the Ford River and the F1 site, along the clear cut for the ELF antenna. The soil was sandy. Three of the hutches were located on top of a hill at the edge of the clear cut west of the antenna, and along an old logging/hunting trail running west from the antenna. Three hutches were located down in a valley east of the antenna (fig. 11). Nearby woods consisted of *Populus tremuloides*, with occasional *Picea glauca*, and *Pinus resinosus*. *Centaurea maculosa* increased from 1983 until it was the most abundant flowering plant on the hill. Also abundant were *Cirsium palustre, Fragaria virginiana, Hieracium aurantiacum, Coronilla varia, Prunus virginiana, Rubus idaeus, Solidago* spp., and *Trifolium* spp.

ELF Antenna Operations

In interpreting results of this project it is important to know the pattern of antennal operations (Fig. 12, 13). The Naval Radio Transmitting Facility in Republic Michigan began testing at 4-10 amperes periodically during the summer (March - October) of 1986, and at 15 amperes with increasing regularity from May, 1987 to June, 1988. Starting July, 1988 and lasting until March, 1989, testing continued at 50% power (75 amperes). In May 1989, the ELF antenna began testing periodically on full power (150 amperes). Continuous full power operation began in October, 1990.

Cumulative potential magnetic field exposure of the bees is plotted in Figs. 12 and 13, based on measurements provided by IITRI (Technical report, ELF Communications System Ecological Monitoring Program: Electromagnetic Field Measurements and Engineering Support), and summarized in Appendices 2 and 3. Unlike electric fields, magnetic fields are not blocked by trees, hutches, or trap nests. Thus magnetic fields are more likely than electric fields to affect the bees. Gauss-Hours of magnetic field exposure of foraging bees during June, July and August are plotted in Fig. 12. A bee sitting directly under the antenna for the entire month would experience the maximum exposure plotted. A bee sitting on the hutch farthest from the antenna at the F2 site would experience the minimum exposure plotted (solid bars). Most bees at the experimental sites would experience intermediate magnetic field exposures while foraging. Figure 13 plots the sum of Gauss-Hours of magnetic field exposure of bee prepupae in overwintering boxes between Sept. and April at the two experimental sites. Exposure of the prepupae at the F2 site was approximately twice that of the F1 site.

In our analyses, 1989 - 1992 are considered full power years and are referred to as "Full" years. Exposures during the intermediate years of 1986-1988 were considerably lower than in subsequent years, and analyses did not show any effect of experimental and control areas on nest architecture and activity. Therefore, we analyze 1983-1988 data as pre-treatment years, and refer to these as "Low" power years. In this context, low includes years before antenna operations.

76 Hz magnetic flux densities at the control sites were 0.001 mG or less during the low power years prior to 1989. During high power years, 76 Hz magnetic flux densities at the control sites reached 0.007 mG at the CL site. One criterion for choosing sites for the ELF projects was that 76Hz field intensities at control sites should be less than 1/10 the intensity at experimental sites at full power. This criterion was easily satisfied for our sites. The experimental site with the lowest 76Hz magnetic flux densities had 330 fold stronger magnetic fields than the control site with the highest 76Hz magnetic flux density in 1992. Similarly, 76Hz magnetic flux densities were at least 39 fold stronger at experimental sites than 60Hz magnetic flux densities at the experimental sites, and at least 770 fold stronger than 60Hz magnetic flux densities at the control sites (Final Technical report, ELF Communications System Ecological Monitoring Program: Electromagnetic Field Measurements and Engineering Support).

Statistical Methods

The General Linear Models (GLM) procedure on SAS for DOS (Version 6.04) was used to analyze sources of variability in cell lengths, leaves per cell, and adult weights (both species), and nest plug length and LO trip durations (*M. inermis*). Because cell lengths, adult weights, or leaves per cell within a nest, and/or LO durations within a cell capping bout, are autocorrelated, we calculate mean cell length, weight, or leaf number for each nest, or mean LO duration for the first three LOs in a cell capping bout. GLM analysis was accomplished on these means. In this model, the error variance includes between nest variability.

In GLM analyses, means of LO duration per cell capping bout were weighted by the number of trip ranks (1-3) that were used to calculate the mean. However, means of cell lengths, adult weights, and leaves per cell were not weighted by number of cells per nest. Rather, cells per nest was a covariate in the models of cell length, adult weight, and leaves per cell.

Incomplete cells (without a cell cap) were not included in calculations of mean cell length for a nest. Not all cells could be measured in some nests, because some of the cells were destroyed by emerging bees. This may have biased the mean cell length of the nest, if most of the unmeasurable cells were inner cells or outer cells. No attempt was made to adjust for such possible biases.

Table 2 summarizes the GLM model that was used to analyze cell lengths, nest plug lengths, leaves per cell, adult weights, and LO durations. Fixed main effects included experimental vs. control areas (referred to as "Exp"), and Antenna operations (Low=1983-1988 or Full=1989-1992). Random nested effects included sites (Site[Exp]), observers or measurers nested in year, and years nested in antenna operations. Where appropriate, other fixed class variables included to explain the variability in the dependent variables were the expected sex of a cell, complete vs. incomplete nests, and early vs. late season nests. Number of cells per nest and nest diameter were covariates in the analysis of cell lengths, adult weights, nest plug lengths, and leaves per cell. Date of the trip was a covariate in the analysis of LO trip durations. Time was tested as a second order covariate in this analysis. Significance would indicate that LO durations are faster (or slower) during the middle of the day, as might be the case if LO durations are correlated with temperature. Type IV mean squares were calculated in all GLM analyses. This model is invariant to the ordering of effects in the model.

The mean square (MS) of Site[Exp] was included in the error term for testing the significance of Exp. This insures that differences between experimental and control areas are significant only if they are greater than any differences between the sites within the areas. The MS of Measurer [Year * Antenna] was included in the error term for testing Year[Antenna], and both Year[Antenna] and Measurer [Year * Antenna] MS were included in the error term for testing the antenna main effect. This insures that differences between years are greater than the differences between measurers who took data in any given year, and that differences between "Full" and "Low" antenna years are greater than the differences between years within those time periods. The GLM procedure calculated appropriate error terms and degrees of freedom for these mixed model analyses using the Random/test statement in SAS.

The most important effect in the GLM model is the interaction term Exp*Antenna. The interaction term was tested with the model error term. If significant, this term indicates that the magnitude of the difference between

treatment and control areas is different during "Full" antenna years than during "Low" antenna years. If the Exp main effect is significant but not the Exp*Antenna interaction, then we know that there are intrinsic differences between experimental and control areas that have nothing to do with the antenna. If the antenna main effect is significant but not the Exp*Antenna interaction, then we know that there are differences between "Low" years and "Full" years that have affected both experimental and control areas equally, as would be the case for climatic changes between years. Ideally, there would be no significant difference between control and experimental areas during "Low" years. If the antenna is having an effect, treatment areas but not control areas should change after the antenna becomes operational and the Exp* Antenna interaction will be significant. This would be the clearest indication that the ELF EM Fields are affecting the bees.

However, a significant Exp*Antenna may also result if control areas change more than treatment areas between "Low" and "Full" years, or if the areas differ before the antenna becomes operational but not after. Such results present an ambiguity. Such results may indicate that ELF EM fields prevented the treatment area from changing (an ELF effect) or that there has been some change in the control areas not related to ELF EM fields (eg., microclimate or vegetation changes). Furthermore, when sample sizes are very large, we must also consider whether a marginally significant effect has biological meaning.

A Shapiro-Wilk statistic for N<51 and a Kolmogorov D statistic for N>=51 in the Univariate procedure of SAS were used to test for normality of residuals in GLM models. The data are tested against a normal distribution with mean and variance equal to the sample mean and variance. The significance level used in these tests was $\alpha = 0.05$. Ln or ln(ln) transformations of the data were sometimes required to meet the assumption of normality of residuals. When used, such transformations are discussed in the Results section. In some cases where residuals were significantly different from normal, a plot of the residuals revealed that a few outliers or a slight skewness of the data were responsible. In these cases the GLM results are likely to be robust, so they are reported. An alternative non-parametric test was tried on nest plug lengths (Zar, 1984 p. 250-251, 221). Lengths were ranked, and the usual GLM model was calculated on the ranks. An H statistic was calculated by dividing the sums of squares from the GLM model by $N(N + 1)/12$, where N is the total sample size. This statistic is closely approximated by χ^2 with degrees of freedom appropriate to the source of variation being tested.

We could not calculate minimum detectable differences for the exp*antenna interaction, but minimum detectable differences between experimental and control areas (Exp) were estimated by year with a modification of Cochran and Cox's formula (Zar, 1984 p.135, 137, 260). Sample size used in this formula was the harmonic mean of the treatment and control area sample sizes (Zar 1984, p. 137) based on numbers actually collected each year for the control and experimental areas. The value of population variance s^2, used in calculating minimum detectable differences was the denominator mean square calculated by the GLM procedure for Exp (Zar, 1984, p. 260). Values of α and the power of the test ($1-\beta$) were 0.05 and 0.9. We hoped to find minimum detectable differences that were no greater than 20% of the mean. When the minimum detectable difference is greater than 20% of the mean, or when the power of the test is less than 0.9, then the parameter may be too variable or potential changes too minor to detect effects of the ELF antenna. When the Exp*Antenna interaction was significant, the actual power of the test could be calculated using the procedure described by Zar (1984 p. 227).

The Categorical Data Modeling (CATMOD) procedure on SAS was used to compare distributions of cells per nest, the proportion of fly parasites vs. other emergences, the proportion of incomplete vs. complete nests, the proportion of males vs. females emerging, and the proportion of prepupal (overwintering) mortality. This statistical program fits linear models to functions of response frequencies for discrete data; i.e., it is an extension of the GLM procedure for continuous data. The program uses a Wald statistic (which approximates a chi-square distribution for large sample sizes) to test hypotheses about linear combinations of the parameters in the model. As with the GLM tests previously described, we tested for significance of experimental vs. control areas (Exp), Sites nested in Exp areas (Site [Exp]), Low power vs. Full power years (Antenna), Year[Antenna], and the interaction between Exp and Antenna (Exp * Antenna). However, a mixed model analysis as was used in GLM analysis is not available with the CATMOD procedure in SAS. The level of significance of all tests was $\alpha = 0.05$. Because of small sample sizes for some site-year categories, we use maximum-likelihood estimates in testing our models. We do not know how to calculate the power of the test in categorical modeling.

Proportion of nests oriented in a N-S vs. E-W direction was tested in a log-likelihood ratio contingency table analysis (Zar 1984, p. 67-68) to determine if the pattern of directions of nests was the same for all years at a given hutch set. If consistency was found between years, then data for a hutch set were pooled over years, and tested against other hutch sets at a given site. If

the ELF antenna was affecting choice of nest direction, then the contingency tests should be significant at some or all of the hutch sets at experimental sites, but not at the control sites. In addition, a change in nest orientations should occur some time between 1988 and 1990. Prior to the change, nest orientation should have been consistent over pre-operational years. Similarly, any changes that occur as a result of ELF EM fields are expected to continue during subsequent operational years.

IV RESULTS ON NEST ARCHITECTURE

Climate, Floral Resources, and Bee Abundance

Table 3 & 4 and Figs. 14 and 15 summarize the number of nests of the two species that had at least one complete cell. Some 1985 *M. inermis* nests are not included in our data analysis because Dr. Fischer, who initiated this research project, used them in experiments on diapause. Data for 1983 are available only for *M. relativa*. Nests were monitored for the entire season only at the F1 site in 1983, and only at two hutches at this site. Some information is also available for late season nests at CL and F2 in 1983. Unfortunately, data for 1984 nests were either not taken, or were unreliable due to personnel problems at the time. Measurement of cell lengths were not taken for 1992 nests, however cells per nest, nest plug lengths, leaves per cell, orientation, sex ratio, and overwintering mortality data were taken for 1992 nests.

Between 1983 and 1992 *M. relativa* produced similar numbers of nests at all sites (17-128), with no consistent differences between control and treatment sites (Fig. 14). In contrast, *M. inermis* produced a consistently lower number of nests at the control sites, especially CL, than at the experimental sites (Fig. 15). Furthermore, *M. inermis* nest numbers at all sites were lower in 1986, 1988 (except for F2), and 1992 than in other years. We believe that these reductions in *M. inermis* populations were caused by a reduction in floral resources due to low rainfall, especially early in the season. Figure 16 plots cumulative precipitation for 1985 - 1992. The first nests of *M. relativa* and *M. inermis* are indicated on the plots, along with first bloom (when known) of two important pollen plants for the bees: *Hieracium aurantiacum*, and *Cirsium palustre*. In 1986, 1988, and 1992 bee nesting and plant flowering began when less than 4 inches of rain had accumulated, whereas in 1985, 1987, and 1989 - 1991 the same events began after 4-5 inches of rain had accumulated. Although no quantitative measures of numbers of flowers in bloom were made, we did note that *H. aurantiacum*, which normally creates a carpet of orange flowers during peak bloom, did not do so in 1986, 1988, and 1992 when very few inflorescences were produced. Thus, newly emerged bees beginning their first nests may have been faced with a dearth of floral resources. *M. inermis* numbers were not affected as strongly at the F2 site in 1988 because of a substantial population of *Centaurea maculosa* that bloomed in late July, in spite of the drought and hot temperatures. This plant was not as abundant at the F2 site in 1986. It is absent from the CL and F1 sites, and was only found

in low numbers at the C5 site in 1988. In 1992, cold temperatures throughout most of the season also kept nest production low.

M. inermis nested later than *M. relativa* (Table 5) by 2 days (1987) to 33 days (1986). *M. relativa* began nesting earlier in 1986-88 than other years. *M. inermis* began nesting earlier in 1987 and later in 1992 than in other years. The midpoint of the season, the date on which 50% of the nests had been started, also varied between years, sites and species (Table 5). This was the last date on which nests were classified as early season nests. Early season ended later for *M. inermis* than for *M. relativa* in all years except 1988.

Hypothesis 1: The average length of cells for each offspring, and/or the average number of cells produced per nest is unchanged by exposure to ELF electromagnetic fields.

M. relativa

The Exp*Antenna interaction was significant for *M. relativa* cell lengths, because cells decreased by a greater amount at the control areas than at experimental areas.

Mean cell length was calculated for each nest, and used in GLM analysis. If ELF EM fields have an effect on cell lengths we would expect to see mean cell lengths changing for the treatment sites but not for the control sites starting in 1989. This does not seem to be the case. There are no consistent trends of differences between experimental and control areas, either in pre-operational years, or under full power in 1989-91 (Fig. 17). Indeed, the means for control and experimental sites overlap considerably both before and after the antenna became operational. Pluses bracketing the means for each year in Fig. 17 indicate upper and lower limits to the minimum detectable differences between control and experimental means for that year. Difference between actual means was always less. GLM analysis (Table 6) confirms that Exp does not contribute significantly to variation in mean cell length. However, Exp * Antenna is significant at the $\alpha = 0.05$ level both with and without expected sex included in the model (Tables 6, 7).

The significant interaction term is due to a greater decrease in cell size between Low and Full power years at the control areas (11.19 mm Low to 10.94 mm Full) than at the experimental areas (11.07 mm Low to 11.00 mm

Full). The change in mean length for the control areas is about 0.2 mm more than the change in mean length for the experimental areas. Note that the control and experimental areas differ more before the antenna was operational (11.19 control vs. 11.07 experimental) than after (10.94 control vs. 11.00 experimental)

Minimum detectable differences for a power of 0.9, calculated by year, were almost all under 20% of the mean, ranging from 3.8% to 9.4% for 1985-1991. However, minimum detectable difference was 24.7% of the mean for 1983 data. The actual difference detected was 1.8% of the mean, a difference that we believe has little biological significance. Effects that have clear biological meaning such as expected sex (females 0.6mm > males, 5.4% of the mean), site (CL=0.25mm larger than other sites, 2.3% of the mean), year (1985 = 0.47mm larger than other years), and season (early season cells = 0.33mm larger than late season cells, 3.0% of the mean) are highly significant ($P<0.0001$, Tables 6, 7. Compared with these large sources of variability, the effect of ELF EM fields, if real, is small.

Overall, the mean cell length per nest was 11.1 mm for *M. relativa* (Table 6). The model accounted for only 16% of the variance in mean cell lengths (see R^2 in Table 6) without expected sex included in the model. When expected sex is included, the model accounts for 27% of the variance (Table 7). The power of the test for Exp*Antenna was only 0.61 - 0.72, less than was used in calculations of minimum detectable differences by year. Female cells averaged 0.6mm larger than male cells (11.55 ± 0.90mm vs. 10.90 ± 0.87mm). Between nest variability (error ms) is large. Cell lengths decreased slightly as diameter increased. In addition, cell length decreased as the number of cells in a nest increased. This may reflect in part a decrease in cell length as cells get closer to the nest entrance. Nests with few cells have large inner cells, so mean cell length is large. Nests with many cells include small cells near the nest entrance, so mean cell length will be lower than for nests with few cells. Cell lengths in early season nests tend to be larger than cells in late season nests. This is contrary to the effect of cells per nest, because early season nests tend to have more cells per nest than do late season nests.

Differences between measurers (Measurer [Year * Antenna]) contributed to variance in mean cell lengths. Mean cell lengths for individual measurers varied from 10.6mm (ND, 1985; BZ 1991) to 11.6mm (VS, 1983) (Table 8).

In summary, *M. relativa* cells decreased by a greater amount at the control areas than at experimental areas (about 0.2mm out of 11.1mm), so that

control and experimental areas were more similar after the antenna became operational than before. ELF EM fields may have prevented a reduction in cell size at the experimental areas that should have occurred, as it did at control areas. A simpler explanation is that change in some factor at the control areas, rather than the ELF EM fields at the experimental areas, is responsible for the significant exp*antenna interaction, if it is real.

M. inermis

The Exp*Antenna interaction was not significant for *M. inermis* cell lengths, indicating that they are not affected by ELF EM fields.

As with *M. relativa* nests, mean cell length was calculated for each nest and used in GLM analysis. However, in some years, numbers of nests are very low at some sites (eg., 1 nest with female cells at the CL site in 1986 and 1988). Therefore, cell length data were pooled for 1985-1986 and for 1987-1988. Only nests with diameters greater than 9.5mm were used in the analysis. This eliminates about 26% of the 1985-1986 nests whose nest diameters were too small to be comparable with nests created after 1986. The residuals were significantly different from normal in this analysis (Kolmogorov D = 0.017 N=3070, P = 0.024), but a histogram of the residuals appeared to be very close to normal, so the GLM results should be accurate.

If ELF EM fields have an effect on *M. inermis* cell lengths we would expect to see mean cell lengths changing consistently for the treatment areas but not for the control areas as ELF EM fields increase. This does not seem to be the case (Fig. 18). GLM analysis (Table 9) confirms that neither Exp nor Exp*Year contribute significantly to variation in mean cell length. Minimum detectable differences for a power of 0.9, calculated by year and sex, ranged from 3.1 to 8.2% of the means, well under the goal of a minimum detectable difference of 20% of the mean. Thus, the chances are good that a biologically significant ELF induced Exp*Year interaction should have been detected. We conclude that ELF EM fields do not influence cell length for this species.

M. inermis cells expected to have female offspring averaged 1.2mm larger than cells expected to have male offspring (16.3mm - 15.2mm). The model accounts for 46% of the variance in mean cell lengths. Parameters that contributed significantly to *M. inermis* cell length were similar to those that were significant for *M. relativa* cell length. Cells from the CL site tended to be significantly larger than cells from C5, and cells from F1 were larger than

cells from F2. Cell lengths decreased slightly as number of cells in a nest increased. Cells in complete nests tended to be larger than cells in incomplete nests.

As with *M. relativa*, differences between measurers (Measurer [Year * Antenna]) made a significant contribution to variance in cell lengths. For example, cells measured by KS were larger than cells measured by other measurers (Table 10).

Number of cells per nest

The Exp*Antenna interaction was not significant for the number of cells per nest, indicating that it is unchanged by exposure to ELF EM fields.

Number of cells per complete nest ranged from 1 to 12 for *M. relativa*. In a CATMOD analysis of cells per nest we used four categories to minimize the cases in which expected frequency was less than five. The categories were: nests with 1 or 2 cells, nests with 3 or 4 cells, nests with 5 or 6 cells, and nests with seven or more cells (Fig. 19).

There were significant differences in the distribution of number of cells per nest between Sites, Years, and Exp areas. However, the interaction between Exp and Antenna was not significant (Table 11), indicating that none of the variability in cells per nest for *M. relativa* can be attributed to antenna operations at the experimental areas.

Number of cells per complete nest ranged from 1 to 8 for *M. inermis*. The deeper the nest, the more cells can be constructed. Therefore, in analyzing cells per nest for *M. inermis*, we compare only 1987 - 1992 nests, when bore depth was routinely 140mm and only drill bits of 11mm were used to make large diameter nests. In all years, the experimental areas have relatively more cells per nest than do control areas (Fig. 20), as confirmed by CATMOD analysis (Table 12) using two categories (1-4 cells or 5-7 cells). No significant Exp * Antenna interaction indicates no effect of ELF EM fields at experimental areas after 1989. The significant "Antenna" effect means that cells per nest differed in 1987 - 1988 as compared with 1989 - 1992 at all sites. Thus, these differences have nothing to do with ELF EM fields.

We do not know how to calculate minimum detectable differences for categorical modeling. However, we reran the CATMOD tests on a data set that was identical to the original data, except that nests from experimental

areas during full power years were decreased by one cell per nest, unless they were already a one-celled nest. For both species, the Exp*Antenna interaction was significant. This suggests that the CATMOD test should have been able to detect a decrease of one cell per nest due to ELF EM fields.

Hypothesis 2. Bees exposed to ELF EM fields, and bees not exposed, will make nest plugs of the same thickness.

The Exp*Antenna interaction for *M. inermis* nest plug lengths was not significant, indicating that plug lengths do not change in response to ELF EM fields. However, differences would have to be as much as 30% of the mean to be detected.

In a GLM analysis similar to those performed on cell lengths, we found that residuals were significantly different from normal (Kolmogorov D = 0.097, N=2600, P <0.01). A histogram of the residuals suggests that the distribution is more leptokurtic than a normal distribution. We have not determined a transformation that would adjust for this problem. However, a GLM of the ranks of nest plug lengths in a non-parametric factorial analysis of the data (Zar 1984 p. 250) give qualitatively identical results as the GLM on the raw data. We present the results from the raw data (Table 13).

If ELF EM fields have an effect on *M. inermis* nest plug lengths we would expect to see nest plug lengths changing consistently for the treatment sites but not for the control sites as ELF EM fields increase. This does not seem to be the case. Control sites had larger nest plugs than experimental sites during some years both before (87+88) and after (89 & 90) the antenna became fully operational (Fig. 21). No pattern was seen some years both before (85+86) and after (90) full antenna operation (Fig. 21). The Exp*Antenna interaction is not significant (Table 13). Ability to detect differences was less than desired particularly during low power years. Minimum detectable difference for a power of 0.9, was 30.2% and 24.0% during low power years (1987 and 1988 respectively), and 12.3 to 16.4% of the mean during the full power years of 1989-1991. Thus, any influence of ELF EM fields on nest plug lengths would have to be fairly large to be detected. No such differences were detected here.

Not surprisingly, cells per nest accounts for the most important contribution to variance in nest plug lengths. Nest plugs average about 7mm less in length as each new cell is added to the nest, presumably because there is less space available in the nest for plug. Nest plug lengths also increase

significantly as diameter increases, and are larger in early season nests. Plugs at the control areas average about 2 mm longer than at experimental areas. Plugs were shorter in 1985 and 1986, presumably because most trap nests were shorter and had fewer cells than in subsequent years (see methods).

Hypothesis 3. The number of leaves used to line a cell is unchanged when bees are exposed to ELF EM fields.

The Exp*Antenna interaction term is significant for *M. inermis*, but not for *M. relativa*. ELF EM fields may be causing *M. inermis* to pad its cells with an extra 0.6 leaf over the average 13 leaves per cell.

Although the number of leaves lining a cell is discrete data, we treat these data as if they were continuous, and use the GLM procedure instead of a CATMOD analysis. This should increase our ability to detect differences between control and experimental areas if any exist.

A mean of ln leaves per cell was calculated for each nest and used in GLM analysis. For *M. relativa*, analysis starts with 1986 data, when leaves were first counted. For *M. inermis*, numbers of nests are very low in some years at some sites (eg., 1 nest with female cells at the CL site in 1986, 1988). Therefore, data on leaves per cell were pooled for pre-operational years 1985-1986 and 1987-1988. Only nests with diameters greater than 9.5mm were used in the *M. inermis* analysis. The residuals were significantly different from normal in the *M. inermis* analysis (Kolmogorov D = 0.018 N=2889, P = 0.021), but a histogram of the residuals appeared to be very close to normal, so the GLM results should be accurate.

If ELF EM fields are having an effect on leaves per cell, we would expect to see mean leaves per cell changing for the treatment sites but not for the control sites as EM fields increase. For *M. relativa*, there were fewer leaves per cell in 1986 and 1987 (Fig. 22) than in subsequent years. However, the magnitude of the changes between low and on antenna years was not significantly different for control and experimental areas (Exp*Antenna F=0.07 df=1 P=0.80; Table 14). The same is true if expected sex was added to the model (Exp*Antenna F=0.06 df=1 P=0.20 Table 15). Minimum detectable differences for a power of 0.9, calculated by year, ranged from 3.5 to 14.1% of the means, within the goal of a minimum detectable difference of 20% of the mean or less. Thus, the chances are good that a biologically significant ELF induced Exp*Year interaction should have been detected. We conclude that

ELF EM fields do not have an effect on leaves per nest for the small bee species.

For *M. inermis*, leaves per cell appears to increase in 1990 and 1991 compared with earlier years (Fig. 23). GLM analysis (Table 16) indicates that the Exp*Antenna interaction is significant for leaves per cell (F=5.58, df=1, P=0.0182). The GLM model estimates that the control areas decrease by 0.1 leaf/cell between low and full power years (13.23 vs. 13.10 leaves), whereas the experimental areas increased by 0.5 leaf/cell between low and full power years (12.49 vs. 13.00 leaves). The control and experimental areas differed more before the antenna became operational (13.23 vs. 12.49 leaves) than they did after the antenna became operational (13.10 vs. 13.00 leaves). This is the reverse of the pattern that we would like to see to explain a significant Exp*Antenna interaction, namely the control and experimental areas being the same before the antenna was operational, and the experimental area changing only after the antenna became operational. The actual results suggest that control areas intrinsically have more leaves per cell than experimental areas, as was apparently the case in 1985-1988, and that *M. inermis* may be padding its cells with an extra 0.6 leaf in the presence of ELF EM fields, so that now there is no difference between experimental and control areas.

Minimum detectable differences for a power of 0.9, calculated by year and sex, were all under 20% of the mean, ranging from 2.3% to 7.5%. The actual difference detected was 2.9% of the mean, with a power of the test for Exp*Antenna of 0.65 for $\alpha = 0.05$.

Unfortunately, sample sizes for *M. inermis* are smallest for the control areas during "low" antenna years of 1985-1988, on which the inference of intrinsic differences between control and experimental areas is based. We would feel more confident that the significant interaction was caused by ELF EM fields if bees were padding their nests in other ways as well. No evidence of such padding was seen in our analysis of *M. inermis* nest plugs.

Despite these caveats, let us assume that bees do increase the leaves per cell by 0.6 leaf in response to ELF EM fields. Does this make a difference? It takes an average of about 2.4 minutes to collect a leaf and about 2.8 minutes to position it in the nest (Strickler, unpublished data). If there are 8 cells in a nest (a maximum), this adds less than 40 minutes to the week or so required to make a nest. The bee population is able to accommodate considerable variability in leaves per cell, and in the time to collect leaves, due to other factors. These include offspring sex (13.9 leaves for male cells, 12.1 leaves for female cells; P<0.0001, Table 16), diameter (about 1.2 leaves per

mm; P<0.0001, Table 16), and intrinsic differences between nests (reflected in the low $R^2 = 0.36$; Table 16). Thus, we expect that an additional 0.6 leaf per cell will have little impact on the total reproductive output of a bee. Our finding of no significant Exp*Antenna interaction in cells per nest for *M. inermis* is consistent with this expectation.

However, the brief additional time out of the nest may increase the risk of exposure of the cell to parasites, to predation or other mortality factors outside of the nest, and/or to usurpation by other species. Risk of parasitism from flies in the genus *Anthrax* spp. is increased by the absence of a female bee at the nest when the cell is being constructed because these parasites flip eggs indiscriminately into unguarded openings (Scott and Strickler, 1992). In contrast, cuckoo bees of the genus *Coelioxys funeraria* tend to lay their eggs just after the *Megachile* lays her egg, not when the cell is being constructed. We used a CATMOD analysis to compare the number of cells containing *Anthrax* parasites to the number of cells with other emergences. There were significant differences between sites and years for *M. inermis* (Site[Exp] χ^2=13.12 df=2 P=0.0014; Year[Antenna] χ^2=39.73 df=6 P<0.0001), but no significant Exp*Antenna interaction (χ^2=0.11 df=1 P=0.7389). Thus, we have no evidence that parasitism increased for *M. inermis* as a result of the addition of an extra leaf per cell in nests constructed under the operational ELF antenna.

There is no direct way to measure predation of bees foraging for leaves, but we can compare the number of incomplete and usurped nests as an indirect measure of such predation. Interestingly, incomplete *M. inermis* nests have significantly more leaves per cell than do complete nests (Table 16; "incomplete" nests includes usurped nests in our analyses). Leaves per cell do not differ for such nests in *M. relativa* (Tables 14, 15). These results are consistent with the possibility that an additional .6 leaf is the cause of the incomplete nests for *M. inermis*. However, in a CATMOD analysis of complete vs. incomplete *M. inermis* nests, the Exp*Antenna interaction was not significant (χ^2=3.56 df=1 P=0.0591). Our data provides no evidence that predation increased as a result of padding cells with an extra leaf.

Hypothesis 4. The relative acceptability of nests oriented in a NS direction vs. nests oriented in an EW direction does not change when bees are exposed to ELF EM fields.

Only one of the 6 hutch sets in the experimental areas showed evidence of a change in nest orientation for *M. relativa* that may be due to ELF

EM fields. The effect of ELF EM fields on nest orientation was minor and locally variable.

As explained in the methods section, at each site there are three sets of hutches. Each hutch set consists of two hutches in close proximity, one oriented NS, and one oriented EW. Nests on the NS hutch have openings facing E or W, while nests on the EW hutch have openings facing N or S. The directions used in this analysis refer to the direction of nest openings.

Each set of hutches is situated in a different location and has a different pattern of sun and shade during the day, and a different compliment of nearby flowering plants. These factors may be important in acceptance of nest opening direction by bees. Thus, we have analyzed nest orientation by hutch set at each site. Furthermore, since sample sizes are low at some hutches in some years, we have not tried to discriminate between nests oriented in four directions; rather we compare acceptance of nests oriented N or S vs. nests oriented E or W. Only data for *M. relativa* are analyzed, since sample size was often low for *M. inermis* at the control areas.

We analyzed the data with a Log-likelihood Ratio (G-test) Contingency test (Table 17). This tests whether the pattern of nest acceptability (whatever the pattern) is the same for all years at a given hutch set. When the null hypothesis was accepted for all hutch sets at a site the data were pooled over years and each hutch set was tested against the other hutch sets at that site, to test whether the pattern was consistent for the entire site.

If ELF EM fields affect nest orientation acceptability, one would expect changes in nest orientation within a hutch set over the years at experimental but not control areas. The results indicate that at three of the four sites there is a consistent bias over all years at a given hutch set, but the bias is different between hutch sets at a given site. These biases are probably due to differences in shading and proximity to resources, which are fairly consistent between years. Only at F1 are there significant changes in orientation within a hutch set over the years. For F1-N, these differences appear to be due to differences between 1985 and subsequent years. If a G-test is repeated with 1985 data removed, the F1-N hutch has a consistent bias (3:9) toward the NS direction ($G=6.681$, $df=6$, $P=0.35$, n.s.). We have no idea why nest directions were different in 1985 than in subsequent years at the F1-N hutch, but this change cannot be related to ELF EM fields. Similarly, nest orientations at the F1-W site have changed in both low power years (eg, 1983 vs. 1985, 1985 vs. 1986, 1988) and full power years (1990 vs. 1991 vs. 1992). Thus, these changes cannot be attributed to ELF EM fields.

For the F1-E hutch set, we compared separately nest orientations in Low power years (1983-1988) and Full power years (1989-1992). Nest orientations were consistent within those groups. During Low power years there was a consistent 3:2 bias toward EW nests (94EW, 65NS; G=7.69, df=4, P=0.103 ns). During Full power years there was a consistent 3:2 bias toward NS nests (16EW, 24NS; G=3.99, df=3, P=0.263 ns). Low and Full power years were significantly different from each other (G=4.71, df=1, P=0.03). Interestingly, the Full power years also saw a decrease in the total numbers of bees nesting at the F1-E hutches (Table 17). It is possible that changes in nest orientation and numbers of nests at the F1-E hutch were caused by local changes in ELF EM fields. However, lack of an effect at other treatment hutches suggests that changes in nest orientation possibly due to ELF EM fields are minor and localized.

V RESULTS ON NEST ACTIVITY

Hypothesis 5. The duration of round leaf (LO) foraging trips remains the same when bees are exposed to ELF EM fields.

The Exp*Antenna interaction was not significant, indicating that ELF EM fields do not affect the duration of LO foraging trips for *M. inermis*. However, differences would have to differ by as much as 29% of the lnln transformed mean to be detected.

During the 1987 field season we noticed that LO trip durations increased with each successive trip after the bee lays her egg. In 1987, however, we did not keep track of which LO trips in the capping sequence were being timed. However, we learned that the female makes a series of very rapid flights in and out of the nest just before collecting the first LO after laying her egg. Undergraduate observers refer to this behavior as "spazzing". Where rapid flights in and out of the nest without a cargo appear at the beginning of a series of 1987 LO timings, we have assumed that the first LO trip for the cell has been timed.

In 1988 we recorded the actual trip number for 73% of the capping sequences that were timed. In 1989 - 1991, we were even more diligent, recording actual trip numbers for every cell cap timed. In our analyses residuals fit a normal distribution when we restrict the analysis to the mean of the first 3 trips if we use a ln(ln) transformation of LO trip durations.

Figure 24 summarizes mean LO durations for the four sites and five years, based on GLM analysis of the mean of trip ranks 1-3 for each cell capping bout. If ELF EM fields were having an effect on LO durations, we would expect to see mean durations increasing (or possibly decreasing) for the treatment sites but not for the control sites since 1989. This does not seem to be the case. LO durations tend to be greater at the experimental sites across all years, even before the antenna became fully operational. Furthermore, mean LO durations have tended to fluctuate around a narrow range of means from year to year. (There was a greater spread between sites in 1987 than in subsequent years because of smaller sample sizes.) Results of the GLM analysis of the mean of trips 1-3 are summarized in Table 18. The error variance is a measure of between bee variability. There is a significant Exp effect, but the interaction between Exp and Antenna does not contribute sig-

nificantly to the variability. Ability to detect differences was less than desired, particularly during low power years. Minimum detectable differences, calculated by year, were 21.8% of the mean (lnln transformed) in 1988, 28.9% in 1989, 10.1% in 1990 and 7.8% in 1991. Thus, any influence of ELF EM fields on LO trip durations would have to be fairly large to be detected. No such differences were detected here.

Time of day did not contribute significantly to variability in LO durations. This suggests that temperature or other weather parameters do not affect LO durations. Date of the timing was significant only in 1990, indicating that in 1990, bees tended to slow down later in the season.

During the summers of 1983-1986, 49 bouts of LO timings were taken for 18 bees. Unfortunately, only 4 of those timing bouts (1 bee) were made at the CL site, and only 2 bouts (1 bee) were timed at the C5 site. Despite the tiny control sample sizes, the GLM was rerun including pooled 1983-1986 data. The interaction term was not significant in this analysis (MS = 0.0017, df = 1, F = 0.023, P = 0.8796), consistent with results for 1987-1991. The date on which timings were made was significant for 1990 and 1983-86 timings.

VI RESULTS ON EMERGENCE

Hypothesis 6. The relative proportions of emerging males and females is unchanged by exposure to ELF EM fields.

The Exp*Antenna interaction was not significant, indicating that *M. relativa* sex ratio was not affected by ELF EM fields.

We have tested this hypothesis with *M. relativa* sex ratio. *M. inermis* data are not suitable for testing this hypothesis because there were changes in nest diameters and depths in 1987 that could affect sex ratio (Stephen and Osgood, 1965). Table 19 presents numbers of males and females emerging, and sex ratios, for each site and year since 1985 for *M. relativa*. There has been much variability between sites and years. Results of categorical modeling of the frequencies of each sex of (Table 20) indicate that there are significant differences between experimental and control areas, between sites, and between years in the relative frequencies of the sexes. However, the Exp * Antenna interaction is not significant, so none of the variability can be attributed to ELF EM fields. Figure 25 illustrates the relative proportions of each sex predicted by the model.

Hypothesis 7. Newly emerged bees exposed to ELF EM fields are the same weight as newly emerged bees not exposed to ELF EM fields.

The Exp*Antenna interaction was not significant, indicating that adult dry weights are not affected by ELF EM fields for either bee species.

Mean adult dry weight for males and females were calculated by nest for each species. In most cases, only one or two bees of each sex were weighed per nest. Means were used in GLM analysis. The Exp*Antenna interaction was not significant in analysis for either bee species (Table 21, 22). For *M. relativa*, minimum detectable differences for a power of 0.9, calculated by year, ranged from 7.4% - 13.9% of the mean, well under the goal of a minimum detectable difference of 20% of the mean. For *M. inermis*, minimum detectable differences, calculated by year and sex, ranged from 6.7% - 19.7% of the mean, except for 1988 females for which the minimum detectable difference was 48.0%. Thus, the chances are good for *M. relativa*, and fair for *M. inermis*, that a biologically significant ELF induced Exp*Year interaction

would have been detected. We conclude that ELF EM fields do not contribute significantly to variability in adult weights.

For both species, sex, Year[Antenna], diameter, and season are the most important factors contributing to variance in adult dry weights (Table 21, 22). The model accounts for 54% of the variance in *M. relativa* dry weights, and 63% of the variance in *M. inermis* dry weights.

After weighing, the bees were pinned and identified. All of the small *Megachile* bees from 1986 - 1990 nests have been confirmed as *M. relativa*. A sample of 1991 - 1992 bees have also been identified and confirmed as *M. relativa* and *M. inermis*. The sample included individuals that were unusual in size or appearance for the species under study.

Hypothesis 8. Overwintering mortality of megachilid bees is unchanged by exposure to ELF EM fields.

For the most part, both species of *Megachile* in our study are univoltine, having only one generation per year. There have been a few exceptions: In *M. relativa* nests, 5 - 22% of all *M. relativa* and 6 - 26% of all *Coelioxys* spp. emergences occur in August and September (Table 23). Far fewer instances of bivoltinism occur in *M. inermis* nests (0 - 0.3%; Table 24). Early emergences do not overwinter, and are not included in the analysis described below.

We have evidence that *M. inermis* but not *M. relativa* overwintering mortality may be increased by ELF EM fields. *M. inermis* mortality at experimental areas increased to the level of control areas, but never increased beyond the level of the control areas. The following discussion explains how we came to that conclusion.

Prior to emergence as an adult in the spring, *Megachile* are subject to a variety of sources of mortality. The egg may fail to hatch, or the larva may die of unknown causes during the summer. The prepupa may die during the winter. The pupa may fail to eclose in the spring. A number of parasites may attack the *Megachile* egg, larva, or pupa at various times in its development. Parasites include the cuckoo bees, *Coelioxys moesta* Cresson on *M. relativa* and *C. funeraria* Smith on both *Megachile* spp.; the flies *Anthrax irroratus irroratus* Say and *Anthrax pluto pluto* Weidemann; chalcid and leucospidid wasps.

The percent mortality due to various causes is presented by site and year for *M. relativa* and *M. inermis* in Tables 25 and 26. Variability between years is due in part to a change in protocol in 1987, leaving nests to overwinter in the field rather than bringing them to Channing. For example, Pre-overwintering mortality (mortality of eggs and larvae) was greater in 1987 than in previous years, and even greater in 1988, especially for *M. relativa*. Weather patterns are undoubtedly also involved. High pre-overwintering mortality in 1988 nests was probably due to dry, hot summer weather. Unusually cold spring weather contributed to overwintering mortality of nests constructed in 1988 and 1989. Numerous summer rainfalls may have caused higher pre-overwintering mortality in 1987 as compared to earlier years. Proportion of adults emerging was particularly low for 1988 *M. relativa* nests.

There are several ways that one can measure overwintering mortality, and several problems that must be dealt with in analyzing it. First, we equate overwintering mortality with the prepupal stage, but actually the prepupa lasts for a longer time than just the winter. The prepupal stage begins several weeks after the egg is laid, when the larva has finished eating its provisions. The prepupa defecates shortly after molting, and then spins a silken cocoon for overwintering that is surrounded by fecal pellets. Thus the prepupal stage may begin as early as mid-summer. It lasts until pupation in the spring. This occurs typically in mid May to late June, although we have opened few cells to find out, to minimize mortality. In spring 1989 - 1993, the prepupal stage for nests constructed in 1988 - 1992 was late compared with 1987 - 1988, due to cool weather and a change in protocol to a shady outdoor emergence site. Figs. 26 - 31 compare emergence of 1987 - 1992 nests in spring of 1988 - 1993. Prior to 1989, pupation and emergence took place in the lab where indoor microclimate and 60 Hz EM fields could affect pupal and adult mortality. Starting in 1989, the effects of 60 Hz EM fields were minimized by moving emergence of all cells to an outdoor holding site.

There is no way to separate prepupal mortality that occurs during the winter from prepupal mortality that occurs in summer, fall or spring. 1987 - 1989 nests were left at the sites where they were constructed during the entire prepupal stage except for the last few weeks, when nests were returned to Crystal Falls for nest architecture measurements. Thus, the effects of ELF EM fields on prepupal mortality any time before May are tested by our protocol.

We have no way of knowing how many adult bees would have successfully emerged at the study sites, but the number of cells that survive past the prepupal stage provides an upper limit. Therefore, we combine pupae,

adults that die in the cocoon, and adults that successfully emerge, into one "post-overwintering" category.

The prepupal stage has the longest duration of all the developmental stages of these univoltine species. However, mortality is usually greater in the pre-overwintering egg and larval stages. Mortality of these early stages show intrinsic differences between sites and differences between years that are weather related (Tables 25, 26), that could make it difficult to detect differences due to ELF EM fields. Therefore, we propose restating our hypothesis as: **Given that a bee survives to the prepupal stage, the probability that it will not survive past the prepupal stage does not change in the presence of ELF EM fields.** Thus, we compare the number of cells with a dead prepupa with the number of cells with post-overwintering bees. Cells containing egg and larval mortality are not included in the analysis.

Parasites present another problem. It is easy to distinguish adult and pupal *Megachile* from adult and pupal parasites. However, we are unable to distinguish prepupae of *Megachile* from prepupae of the cuckoo bee, *Coelioxys* (also in the Megachilidae). The *Coelioxys* larva kills its host larva or egg, and feeds on the provisions in the cell. Like the host bee, *Coelioxys* overwinters in the prepupal stage. When testing the hypothesis above, the number of cells with dead prepupae should be reduced by the percentage of cells that are parasitized by *Coelioxys*, but this is difficult to determine. Therefore, we have not tried to separate *Megachile* and *Coelioxys* data. Rather, we assume that both genera are affected in the same ways, if at all, by ELF EM fields. This assumption is more likely to be true for two bee species in the megachilid family, than for a bee and a fly or wasp parasite. Thus, both adult *Megachile* and adult *Coelioxys* are included in the category of bees that survived the winter.

In 1989, prepupal mortality often occurred in several cells in a row in a nest. Some of these cells had a partially formed pupa visible under the prepupa exoskeleton. These prepupae obviously died late in their development, just before pupation (when not exposed to ELF EM fields). We believe this occurred during the cold spring weather, particularly on May 10, when there was a snow storm. The bees within a nest tend to emerge within two or three days of each other, although emergence of the entire population takes much longer. This suggests that development is synchronous within a nest, so that mortality at critical stages of development may be autocorrelated. For 1989 nests in particular, prepupal mortality in a cell was probably not independent of prepupal mortality of other cells in the same nest, which were all at the same stage of development when cold weather occurred. Therefore, in addi-

tion to an analysis of prepupal mortality by cells, we have analyzed prepupal mortality by nest. Percent of nests with prepupal mortality for each site and year is defined as number of nests containing at least one dead prepupa divided by all nests with at least one *Megachile* or *Coelioxys* prepupa or post-overwintering stage x 100.

1985 and 1986 nests were not overwintered at the sites where they were constructed. Therefore, analyses of prepupal mortality include only nests constructed between 1987 and 1992. This analysis includes 2 "Low" antenna years and 4 "Full" antenna years. If ELF EM fields are having an effect on overwintering mortality, we would expect to see changes in mortality at the treatment sites but not at the control sites after the antenna became operational.

Exp*Antenna did not contribute significantly to variance in proportion of cells or nests with prepupal mortality for *M. relativa* (Tables 27, 28). This suggests that exposure to ELF EM fields during the winters of 1989-90, 1990-91, 1991-92, and 1992-93 did not affect overwintering mortality. Year was significant in all tests, as can be seen in prepupal mortality predicted by the model (Figs. 32 and 33). However, the differences do not correspond to the operational status of the ELF antenna.

The Exp * Antenna term is significant for *M. inermis* cells and nests (Tables 29, 30). Examination of prepupal mortalities predicted by the model (Figs. 34 and 35) suggests that the percent of cells and nests with prepupal mortality increased more at the experimental areas after the antenna became operational than at the control areas. Before the antenna was operational, overwintering mortality at the experimental areas was about 60% of the mortality at the control areas. After the antenna became operational, mortality at experimental areas has been about the same as at control areas. This suggests that there is an intrinsic difference between the control and experimental areas that disappeared on exposure to ELF EM fields. This is the reverse of the pattern that we would like to see to explain a significant Exp*Antenna interaction, namely the control and experimental areas being the same before the antenna was operational, and the experimental area changing only after the antenna became operational.

Unfortunately, sample sizes for *M. inermis* are smallest at control areas during Low power years, on which the inference of intrinsic differences between control and experimental areas is based, and data is available for only two Low power years. Thus, it is possible that the null hypothesis of no difference between control and experimental areas was incorrectly rejected.

Note that mortality at the experimental areas never exceeded the mortality at the control areas. If it had this would have been a less ambiguous indicator of an ELF effect.

In the manipulative experiment, nests (and cells) constructed at the F2 site but overwintered at the C5 site, had mortality closer to nests constructed and overwintered at C5 than to nests constructed and overwintered at F2 (Fig. 36, Table 31). This indicates that winter conditions at the F2 experimental site caused greater prepupal mortality in 1990 and 1991 than did conditions at the C5 control site. One such condition may be exposure to ELF EM fields.

In summary, *M. inermis* but not *M. relativa* overwintering mortality may be increased by ELF EM fields. *M. inermis* mortality at experimental areas was 60% of the mortality at control areas before the antenna became operational. Mortality increased to the level of control areas, but never increased beyond the level of the control areas, after the antenna became operational.

VII SUMMARY AND CONCLUSIONS

Studies of the effects of high voltage transmission lines and magnetic fields in honeybees suggest several ways that solitary megachilid bees might be affected by ELF electromagnetic fields. In particular, honeybees show greater levels of activity, reduced reproductive output, lower overwintering survival and modifications of nest structure in response to high voltage transmission lines. In addition, honeybees can detect magnetic fields and may use them in orientation. ELF EM fields may affect megachilid bees in similar ways.

Megachilid bees are particularly well suited for this study. Their investment per offspring and reproductive output per nest are easy to measure because they provide each offspring with a discrete cell, and because they readily nest in artificial nests. Three types of data have been gathered in past years: nest architecture, nest activity, and emergence/mortality.

Two species at the experimental and control areas, both in the genus *Megachile*, are the focus of our analysis. As members of the same subgenus of Megachile, with similar behavior, they may be impacted in similar ways by ELF EM fields. However, these species differ in size and degree of sexual dimorphism. Because adult size is correlated with larval provisions, and thus with parental foraging behavior, the species may be impacted in some ways differently by ELF EM fields.

If ELF EM fields affect leafcutting bees, they are likely to disorient or slow foraging bees, or increase stress on bees in the nest, possibly leading to increased mortality. The hypotheses that test for these effects and their results for the two bee species studied, are summarized in Table 32.

If foraging bees are disoriented or slowed, this could reduce foraging time directly (hypothesis 5), and/or cause a reduction in parental investment in offspring. Such changes would be reflected in reduced cell size, reduced numbers of cells per nest (hypothesis 1), an increased proportion of male offspring (which require less investment than females) (hypothesis 6), and/or a decrease in adult offspring body weight (hypothesis 7). These changes could have long term detrimental effects on bee populations. The strongest evidence that the ELF antenna affects orientation and/or parental investment would be significant results for several or all of this suite of related variables.

None of the potential changes in foraging rate or parental investment was detected in this study. While differences between sites and years were significant for many of the variables tested, none of the changes was consistently associated with experimental areas in years when the antenna was operational. The Exp* Antenna interaction was significant for cell length for the small bee species, *M. relativa*, but this was caused by a 0.2 mm greater decrease at control areas than at experimental areas between low and full power years. This suggests that some factor was affecting the control areas, rather than ELF EM fields affecting experimental areas. The magnitude of this change is small (1.8% of the mean), less than differences between sex and season which are known to be related to investment in offspring. Nothing like the halving of colony weight, or complete cessation of reproduction that was observed in honeybee colonies (see introduction) was observed with the *Megachile*. Generally, differences between experimental and control areas of 20% of the mean or less could be detected in our tests, though detectable differences were closer to 30% of the mean for round-leaf foraging durations.

Honeybees responded to stress from electric fields under high tension power lines by increasing the propolis in their nest, so it is possible that leaf-cutting bees might respond with additional leaves in their cells (hypothesis 3) or nest plugs (hypothesis 2). Nest orientation might also change in response to stress from ELF EM fields. No significant changes in leaves per cell were detected for *M. relativa* nests exposed to ELF EM fields. The larger bee species, *M. inermis*, showed an increase of an average of 0.6 leaf per cell (2.9% of the mean) when exposed to ELF EM fields. This finding is based on greater differences between control and experimental areas during low power years, and no differences during full power years. However, low population numbers at control areas before the antenna was operational leave some question as to whether control areas really differed from experimental areas in early years of the study.

Only one of 6 sets of hutches at experimental areas showed a change in nest orientation that might be due to ELF EM fields. No evidence was found of increased padding in the nest plug, although differences would have to be 30% of the mean to be detectable.

At worst, stress from ELF EM fields might increase overwintering mortality (hypothesis 8). Honeybee mortality more than doubled (from 29% when shielded to 71% when not shielded, Greenberg et al., 1981) under high voltage transmission lines. We observed no change in *M. relativa* mortality that could be attributed to ELF EM fields. *M. inermis* mortality increased from 60% of control mortality before the antenna became fully operational, to

no differences in mortality after. This increase in mortality may have been due to ELF EM fields. However, our estimate of differences in mortality before the antenna became operational is questionable because of low sample sizes at the control areas, and only two years of low power data.

In summary, a few minor changes in bee nesting biology and survival may have occurred due to ELF EM fields. All of the significant changes were small in magnitude, sporadic, localized, not consistent between species, and do not suggest a pattern of impact due to disorientation, reduced parental investment in offspring, or response to stress. Significant effects often involved greater differences during low power years between control and experimental areas than during full power years. Since sample sizes were small for the controls during low power years, the reliability of these differences is questionable. These changes are not large enough or consistent enough to raise concerns about the impact of ELF EM fields on Megachilid bees.

VIII REFERENCES

Alcock, J. 1979. The relation between female body size and provisioning behavior in the bee *Centris palida* Fox (Hymenoptera: Anthophoridae). J. Kansas Ent. Soc. 52:623-632.

Baird, C. R. and R. M. Bitner. 1991. Loose cell management of leafcutting bees. Western Regional Extension Publication 12. 7pp.

Bindokas, V. P., J. R. Gauger, and B. Greenberg. 1988. Mechanism of biological effects observed in honeybees (*Apis mellifera* L.) hived under extra-high-voltage transmission lines: implications derived from bee exposure to simulated intense electric fields and shocks. Bioelectromagnetics 9:285-301.

Bohart, G. E. 1972. Managing wild bees for crop pollination. Ann. Rev. Entomol.

Bohart, G. E. and G. F. Knowlton. 1964. Managing the leaf-cutting bee for higher alfalfa seed yields. Utah Ag. Expt. Sta. Circ. 144.

Cowan, D. P. 1981. Parental investment in two solitary wasps, *Ancistrocerus adiabatus*, and *Euodynerus foraminatus* (Eumenidae: Hymenoptera). Behav. Ecol. and Sociobio. 9:95-102.

Danforth, B. N. 1990. Provisioning behavior and the estimation of investment ratios in a solitary bee, *Calliopsis (Hypomacrotera) persimilis* (Cockerell) (Hymenoptera: Andrenidae). Behav. Ecol. and Sociobio. 27:159-168.

Erickson, E. H. 1975. Surface electric potentials on worker honeybees leaving and entering the hive. J. Apicultural Res. 14:141-147.

Erickson, E. H. 1982. Evidence for electrostatic enhancement of odor receptor function by worker honeybee antennae. Bioelectromagnetics 3:413-420.

Erickson, E. H. and S. L. Buchmann. 1983. Electrostatics and Pollination. In: C. E. Jones and R. J. Little, eds. Handbook of Experimental Pollination Biology. Van Nostrand Reinhold Co. N.Y. pp.173-184.

Gerber, H. S. and E. C. Klostermeyer. 1972. Factors affecting the sex ratio and nesting behavior of the alfalfa leafcutter bee. Wash. Ag. Expt. Sta. Tech. Bull. 73. 11pp.

Gould, J. L. 1980. The case for magnetic sensitivity in birds and bees (such as it is). Am. Sci. 68:256-67.

Gould, J. L., L. Kirschvink, and K. S. Deffeyes. 1978. Bees have magnetic remanence. Science 102:1026-28.

Gould, J. L., L. Kirschvink, K. S. Deffeyes, and M. L. Brines. 1980. Orientation of demagnetized bees. J. exp. biol. 86:1-8.

Greenberg, B., V. P. Bindokas, M. J. Frazier, and J. R. Gauger. 1981. Response of Honey Bees, Apis mellifera L., to high-voltage transmission lines. Environ. Entomol. 10: 600-610.

Hobbs, G. A. 1972 Beekeeping with alfalfa leafcutter bees in Canada. Bee World 53:167-173.

Johansen, C. A., E. C. Klostermeyer, J. D. Eves, and H. S. Gerber. 1969. Suggestions on alfalfa leafcutter bee management. Wash. Coop. Ext. Serv. EM 2775.

Johnson, M. D. 1988. The relationship of provision weight to adult weight and sex ratio in the solitary bee, *Ceratina calcarata*. Ecol. Entomol. 13:165-170.

Klostermeyer, E. C., S. J. Mech Jr., and W. B. Rasmussen. 1973. Sex and weight of *Megachile rotundata* progeny associated with provision weights. J. Kansas Entomol. Soc. 46:536-48.

Klostermeyer, E. C., and H. S. Gerber. 1970. Sex control by bees: A voluntary act of egg fertilization during oviposition. Science 167:82-84.

Kirschvink, J. L., and A. K. Kirschvink. 1991. Is Geomagnetic sensitivity real? Replication of the Walker-Bitterman magnetic conditioning experiment in honey bees. Amer. Zool. 31:169-185.

Krombein, K. V. 1967. Trap-nesting wasps and bees: life histories, nests, and associates. Smithsonian Press, Washington, D. C. 570p.

Leucht, T. H. and H. Martin. 1990. Interactions between e-vector orientation and weak, steady magnetic fields in the honeybee, *Apis mellifica*. Naturwissenschaften. 77:130-133.

Longair, R. W. 1981. Sex ratio variations in xylophilous aculeate Hymenoptera. Evolution. 35:597-600.

Medler, J. T. 1958. A note on *Megachile inermis* Prov. in trap-nests in Wisconsin (Hymenoptera: Megachilidae) Canad. Entomol. 90:325-327.

Medler, J. T. and T. W. Koerber. 1958. Biology of *Megachile relativa* Cresson (Hymenoptera: Megachilidae) in trap-nests in Wisconsin. Ann. Entomol. Soc. Am. 51:337-344.

Mitchell, T. B. 1962. Bees of the Eastern United States Vol. II. North Carolina Agric. Exp. Sta. Tech. Bull. No. 152. pp. 108-191.

Scott, V. L. and K. Strickler. 1992. New host records for two species of *Anthrax* (Diptera: Bombyliidae). J. Kansas Entomol. Soc. 65:393-402.

Stephen, W. P. 1955. Alfalfa pollination in Manitoba. J. Econ. Entomol. 48:543-548.

Stephen, W. P. 1956. Notes on the biologies of *Megachile frigida* Smith and *M. inermis* Provancher (Hymenoptera: Megachilidae). Pan Pacific Entomol. 32:95-101.

Stephen, W. P. 1962. Propagation of the leaf-cutter bee for alfalfa seed production. Oregon Ag. Expt. Sta. Bull. 586.

Stephen, W. P. 1981. The design and function of field domiciles and incubators for leafcutting bee management (*Megachile rotundata* (Fabricius)). Oregon State University Agricultural Experiment Station Bulletin 654. 13pp.

Stephen, W. P. and C. E. Osgood. 1965. Influence of tunnel size and nesting medium on sex ratios in a leaf-cutter bee, *Megachile rotundata*. J. Econ. Entomol. 58:965-968.

Strickler, K. 1979. Specialization and foraging efficiency of solitary bees. Ecology 60:998-1009.

Strickler, K. 1982. Parental investment per offspring by a specialist bee: does it change seasonally? Evolution 36:1098-1100.

Sugiura, N. and Y. Maeta. 1989. Parental investment and offspring sex ratio in a solitary Mason Bee, *Osmia cornifrons* (Radoszkowski) (Hymenoptera, Megachilidae). Jpn. J. Entomol. 57:861-875.

Tepedino, V. J. and P. F. Torchio. 1982. Phenotypic variability in nesting success among *Osmia lignaria propinqua* females in a glasshouse environment (Hymenoptera: Megachilidae). Ecol. Entomol. 7:453-462.

Tepedino, V. J. and P. F. Torchio. 1989. Influence of nest hole selection on sex ratio and progeny size in *Osmia lignaria propinqua* (Hymenoptera: Megachilidae). Ann. Entomol. Soc. Am. 82:355-360.

Tomlinson, J., S. McGinty, and J. Kish. 1981. Magnets curtail Honey Bee dancing. Animal Behaviour 29:307-8.

Torchio, P. F. 1981a. Field experiments with *Osmia lignaria propinqua* Cresson as a pollinator in almond orchards: I. 1975 studies. J. Kansas Entomol. Soc. 54:815-823.

Torchio, P. F. 1981b. Field experiments with *Osmia lignaria propinqua* Cresson as a pollinator in almond orchards: II. 1976 studies. J. Kansas Entomol. Soc. 54:824-836.

Torchio, P. F. 1982a. Field experiments with *Osmia lignaria propinqua* Cresson as a pollinator in almond orchards: III. 1977 studies. J. Kansas Entomol. Soc. 55:101-116.

Torchio, P. F. 1982b. Field experiments with a pollinator species, *Osmia lignaria propinqua* Cresson, in apple orchards: I. 1975 studies. J. Kansas Entomol. Soc. 55:136-144.

Torchio, P. F. 1982c. Field experiments with a pollinator species, *Osmia lignaria propinqua* Cresson, in apple orchards: II. 1976 studies. J. Kansas Entomol. Soc. 55:759-778.

Torchio, P. F. 1984a. Field experiments with a pollinator species, *Osmia lignaria propinqua* Cresson, in apple orchards: III. 1977 studies. J. Kansas Entomol. Soc. 57:517-521.

Torchio, P. F. 1984b. Field experiments with a pollinator species, *Osmia lignaria propinqua* Cresson, in apple orchards: IV. 1978 studies. J. Kansas Entomol. Soc. 57:689-694.

Torchio, P. F. 1985. Field experiments with a pollinator species, *Osmia lignaria propinqua* Cresson, in apple orchards: V. (1979-1980), methods of introducing bees, nesting success, seed counts, fruit yields (Hymenoptera: Megachilidae). J. Kansas Entomol. Soc. 58:448-464.

Torchio, P. F. and V. J. Tepedino. 1980. Sex ratio, body size, and seasonality in a solitary bee, *Osmia lignaria propinqua* Cresson (Hymenoptera: Megachilidae). Evolution 34: 993-1003.

Trivers, R. L. and H. Hare. 1976. Haplodiploidy and the evolution of the social insects. Science 191:249-263.

Walker, M. M. and M. E. Bitterman. 1989. Conditioning analysis of magnetoreception in honeybees. Bioelectromagnetics 10:261-275.

Wellenstein, G. 1973. Der einflus von hochspannungs-leitungen auf bienenvolker (*Apis mellifica* L.). Z. ang. Ent. 74:86-94.

Zar, J. H. 1984. Biostatistical Analysis 2nd Ed. Prentice-Hall, N.J. 718pp.

IX APPENDIX 1: PUBLICATIONS AND PRESENTATIONS

Publications:

Scott, V. and K. Strickler. 1992. New host records for two species of *Anthrax* (Diptera: Bombyliidae). J. Kansas Ent. Soc. 65: 393-402.

Scott, V.L. 1994. Phenology and trap selection of three species of *Hylaeus* (Hymenoptera: Colletidae) in Upper Michigan. Great Lakes Entomol. in press.

Strickler, K., V.L. Scott, and R. L. Fischer. In Prep. Comparative nest architecture of two sympatric leafcutting bees that differ in body size (Hymenoptera: Megachilidae).

Presentations:

Strickler, K. 1987. Progress on Native Bee Project Research. ELF Communication System Ecological Monitoring Project Technical Symposium, Cable, WI.

Strickler, K., R.L. Fischer, J. Zablotny, and S. Ozminski. 1987. Implications of body size for partitioning resources among offspring in two species of leaf-cutter bees (Apoidea: Megachilidae). National Meeting, Ecol. Soc. Amer., Columbus, OH.

Scott, V.L. and K. Strickler. 1987. Nest architecture and sex ratio in two species of yellow-faced bees (Apoidea: Colletidae). National Meeting, Ecol. Soc. Amer., Columbus, OH.

Strickler, K., R.L. Fischer, J. Zablotny, and S. Ozminski. 1987. Body size and partitioning of resources among offspring in leaf-cutter bees. National Meeting, Ent. Soc. Amer., Boston, MA.

Strickler, K. 1988. Progress on Native Bee Project Research. ELF Communication System Ecological Monitoring Project Technical Symposium, Traverse City, MI.

Strickler, K. 1988. Nesting behavior of two species of leafcutter bees at the ELF Communications System Facility in Northern Michigan (Hymenoptera: Megachilidae). XVIII International Congress of Entomology, Vancouver, BC, Canada.

Strickler, K. 1989. Progress on Native Bee Project Research. ELF Communication System Ecological Monitoring Project Technical Symposium, Cable, WI.

MacLachlan, B.Z. & K. Strickler. 1989. Do diploid males occur among Megachilids? National Meeting Ent. Soc. Amer. San Antonio, TX.

Strickler, K. 1990. Progress on Native Bee Project Research. ELF Communication System Ecological Monitoring Project Technical Symposium, Houghton, MI.

Strickler, K. 1991. Progress on Native Bee Project Research. ELF Communication System Ecological Monitoring Project Technical Symposium, Lansing, MI.

Strickler, K., V. Scott & D. Dale. 1991. Leafcutter bee nests as folk art - individual variability in Megachile inermis nests. Poster Session, National Meeting Ent. Soc. Amerc. Reno, NV.

Strickler, K. 1992. Progress on Native Bee Project Research. ELF Communication System Ecological Monitoring Project Technical Symposium, Shanty Creek Resort, MI.

Strickler, K., V. Scott & D. Dale. 1992. Leafcutter bee nests as folk art - individual variability in Megachile inermis nests. Poster Session, International Workshop on Non-Apis Bees and Their Role as Crop Pollinators, Logan, UT.

Strickler, K., & V. Scott. 1992. Nesting ecology of two leafcutter bee species in Upper Michigan. International Workshop on Non-Apis Bees and Their Role as Crop Pollinators, Logan, UT.

Scott, V., & K. Strickler. 1992. Coelioxys parasitism of Megachile nests in Upper Michigan. International Workshop on Non-Apis Bees and Their Role as Crop Pollinators, Logan, UT.

Strickler, K. 1993. Progress on Native Bee Project Research. ELF Communication System Ecological Monitoring Project Technical Symposium, Sault Ste. Marie, MI.

Strickler, K. & V. Scott. 1993. Body size and response to stress in two species of leafcutting bee (Hymenoptera: Megachilidae). Ecological Society of America, Madison, WI.

Strickler, K. 1994. Final Report on Native Bee Project Research. ELF Communication System Ecological Monitoring Project Technical Symposium, Bethesda, MD.

X APPENDIX 2: SITES F1 AND F2 EM EXPOSURE PARAMETERS - SUMMER NESTING SEASON

Year	Antenna	Hours of Operation			Magnetic Flux Density (mG)		Cumulative Exposure (mG-hours) Max. under the antenna (F1)			Min. at furthest hutch (F2-N)		
		June	July	August	Max.	Min.	June	July	August	June	July	August
1986	NS	0	24	17	0.770	0.060	0	19	13	0	1.5	1
	N EW	19	14	0.4	0.024	0.002	0.5	0	0	0	0.3	0
	S EW	12	0	0.7	0.004	--	0	0	0	-	-	-
							0.5	19	13	0	1.8	1
1987	NS	44	28	32	3.10	0.22	138	86	100	10	6	7
	EW	44	29	32	0.004	0.002	0	0	0	1	0	0
							138	86	100.	11	6	7
1988	NS	43	40	60	14.4	1.05	623	582	859	45	43	63
	EW	43	43	69	0.052	0.005	2	2	4	0	0	0
							625	584	863	46	43	63
1989	NS	3	14	40	28.8	2.1	84	405	1,152	6	30	84
	EW	4	17	30	0.104	0.01	0	2	3	0	0	0
	Both	526	608	499	31	2.1	16,299	18,838	15,477	1,104	1,276	1,048
							16,383	19,245	16,632	1,110	1,306	1,132

Year	Antenna	Hours of Operation			Magnetic Flux Density (mG)		Cumulative Exposure (mG-hours) Max. under the antenna (F1)			Min. at furthest hutch (F2-N)		
		June	July	August	Max.	Min.	June	July	August	June	July	August
1990	NS	0.6	5	105	28.8	2.1	16	146	2946	1	11	221
	EW	0.7	0	0.5	0.104	0.01	0	0	0	0	0	0
	Both	684	705	596	29	2.1	19,848	20,436	17,293	1,437	1,480	1,252
							19,864	20,582	20,239	1,438	1,491	1,473
1991	NS	663	225	17	28	2.2	18,576	6307	471	1,393	473	35
	EW	0	4	2	0.104	0.01	0	0	0	0	0	0
	Both	0	453	637	27	2.2	0	12,226	17,205	0	951	1,338
							18,576	18,533	17,676	1,393	1,424	1,373
1992	NS	0	0	10	32	2.3	0	9	309	0	1	22
	EW	0	0	6	0.104	0.01	0	0	1	0		0
	Both	348	633	702	32	2.3	11,143	20,243	22,457	801	1,455	1,614
							11,143	20,252	22,767	801	1,456	1,636

XI APPENDIX 3: SITES F1 AND F2 EM EXPOSURE PARAMETERS - WINTER MONTHS

Winter of	Antenna	Hours of Operation Sept. - April	Magnetic Flux Density (mG) F1	F2	Cumulative Exposure (mG-hours) F1 Overwintering Site *	F2 Overwintering Site **
1987-88	NS	209	0.72	1.33	149	277
	EW	218	0.004	0.002	1	0
					150	277

		Sept.-March	April	S-M , A	S-M , A	Sept.-March	April	Sept.-March	April
1988-89									
	NS	309	1	3.2 , 6.4	6.2 , 12.4	988	7	1,913	14
	EW	313	3	0.016	0.026	5	0.	8	0
	Both		7.	-- , 6.6	-- , 12.8	--	48	--	93
							1048		2029

1989-90	NS	45	6.4	12.4	290	561	
	EW	179	0.032	0.052	5	9	
	Both	5,166	6.5	12.8	33,578	66,123	
					33,873	66,693	

Winter of	Antenna	Hours of Operation Sept. - April		Magnetic Flux Density (mG) F1	F2	Cumulative Exposure (mG-hours) F1 Overwintering Site *		F2 Overwintering Site **	
1990-91	NS	23		6.4	12.4	146		283	
	EW	9		0.032	0.052	0		0	
	Both	5,184		6.4	12.8	33,179		66,658	
						33,325		66,941	
		1991	1992	91 , 92	91 , 92	1991	1992	1991	1992
1991-92	NS	165	1,899	6.1, 6.6	11.8, 12.8	1,005	12,535	1,944	24,311
	EW	6	0	0.032	0.052	0	0	0	0
	Both	2,475	3,250	6.1, 6.6	11.8, 12.8	15,095	5,119	29,199	9,929
							33,754		65,383
1992-93	NS	1		6.6	12.8	8		15	
	EW	6		0.032	0.052	0		0	
	Both	5,339		6.6	12.8	35,236		68,336	
						35,244		68,351	

* Actual measurements were made at the F1 overwintering site in 1988- 1992. Estimated in 1987 from intensities at the nearest hutch (F1-E), multiplied by 2.17, the ratio between the overwintering site and F1-E, in subsequent years.
** Actual measurements at the exact overwintering site were not made. The intensities used here were measured at the nearby F2-W hutch.

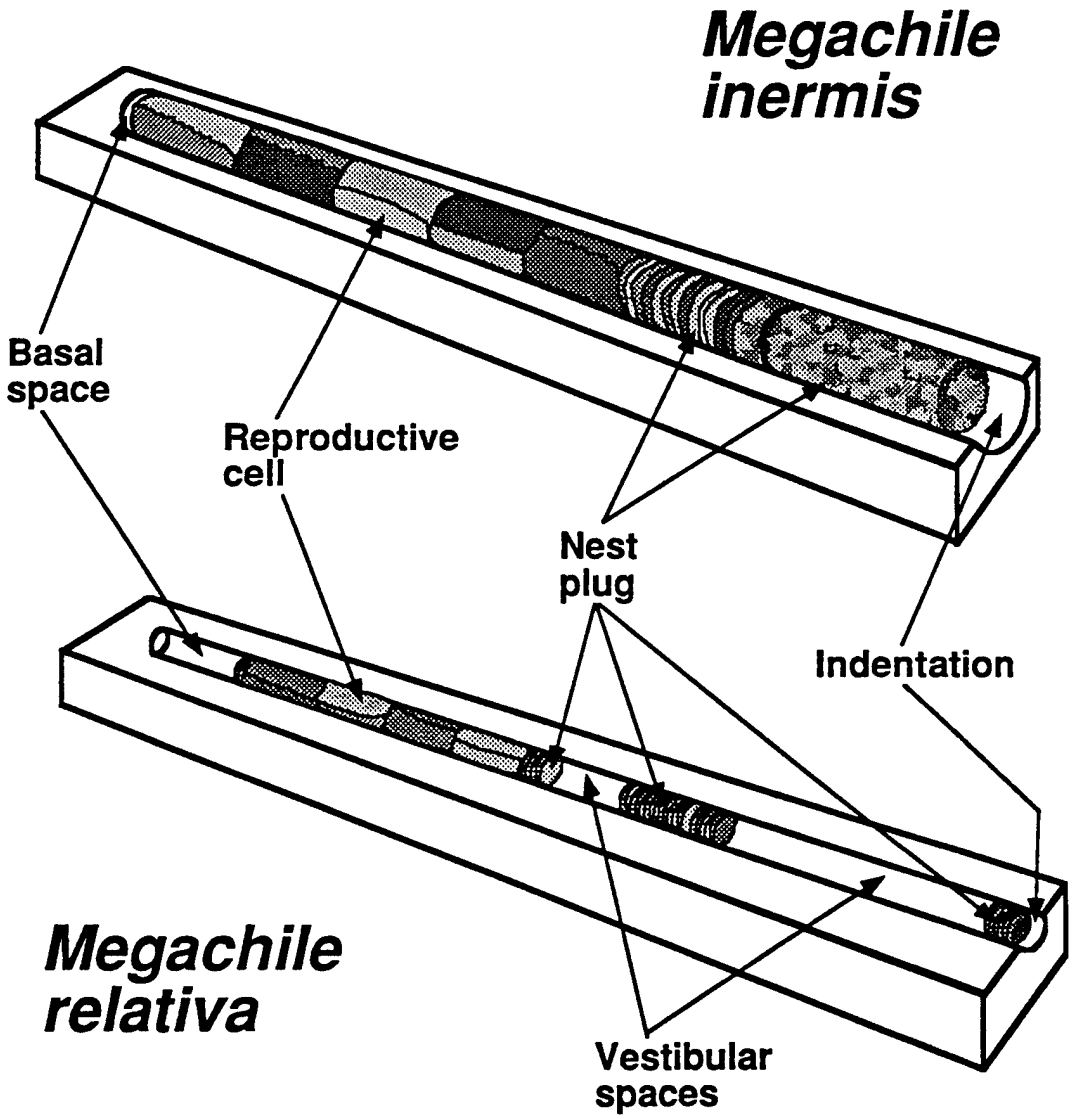


FIGURE 1. Cut away view of a completed *Megachile inermis* and a completed *M. relativa* nest.

TABLE 1. Diameter of drill bits used to create trap nests.

Diameter, mm	Used by *M. relativa*	Used by *M. inermis*
4.4*		
5.2*	xx	
5.5	xxx	
6.0	xxx	
7.2*	xx	x
9.4*		xx
11.0		xxx

* Drill bit diameters used before 1987 only.

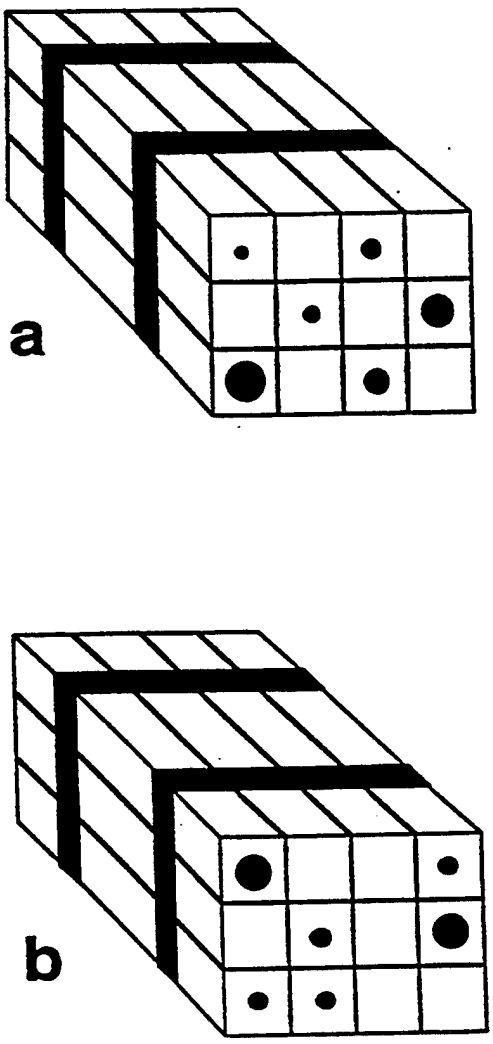


FIGURE 2. Examples of arrangement of nests in a block.
a) 1983 - 1986. b) 1987 - 1992.

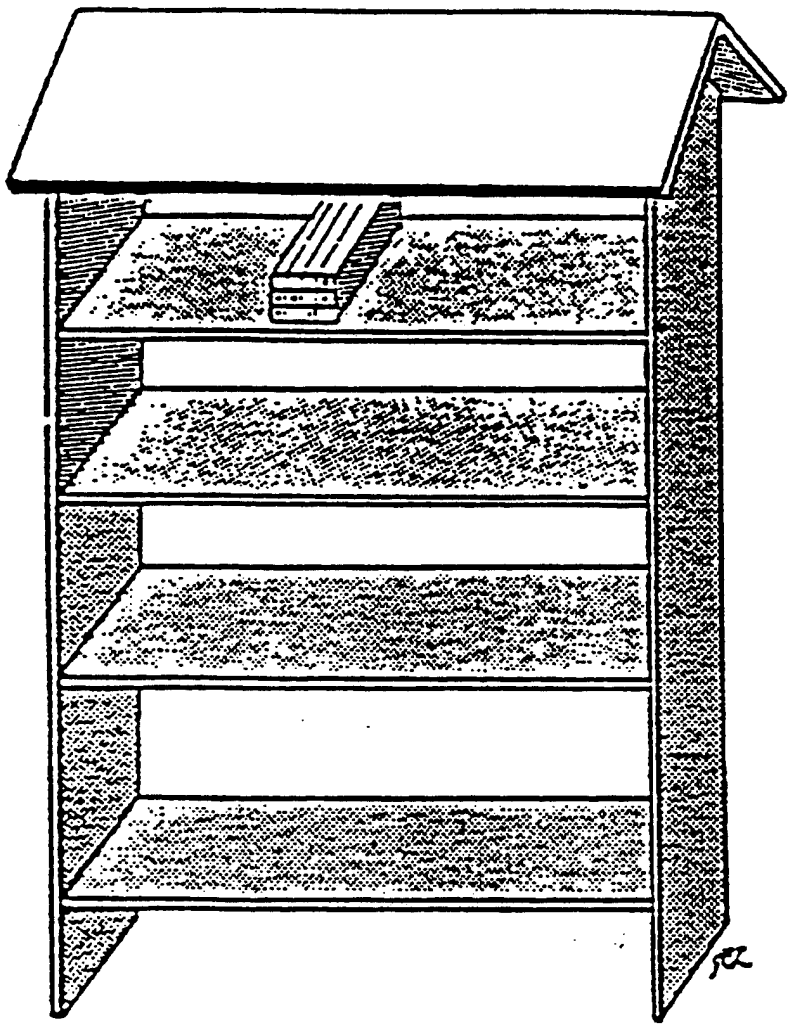


FIGURE 3. Hutch, with one block of nests.

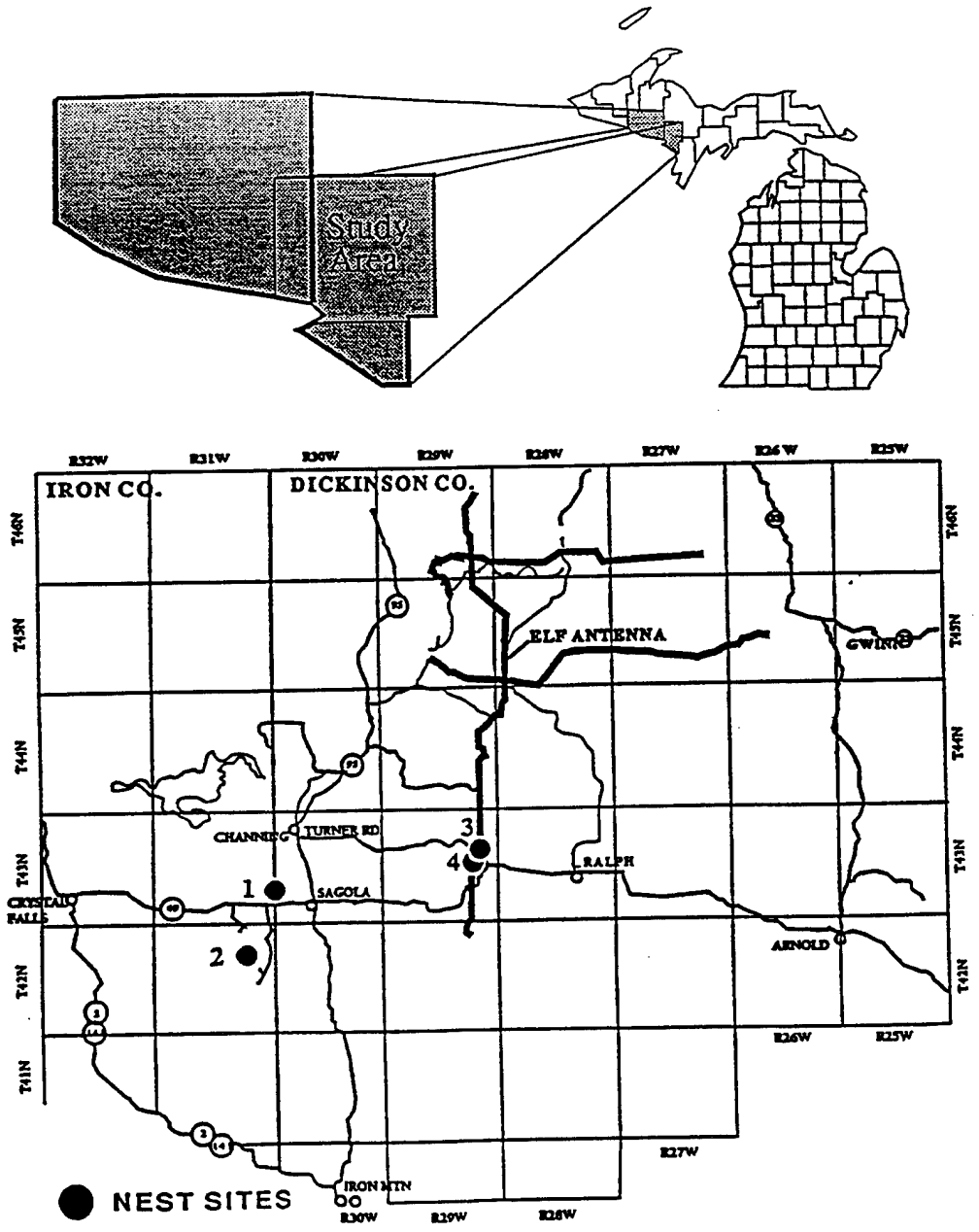


FIGURE 4. Map of the study areas in Iron and Dickinson Co. in Michigan's Upper Peninsula.
Control sites: Site 1 = CL, Site 2 = C5. Experimental sites: Site 3 = F1, Site 4 = F2.

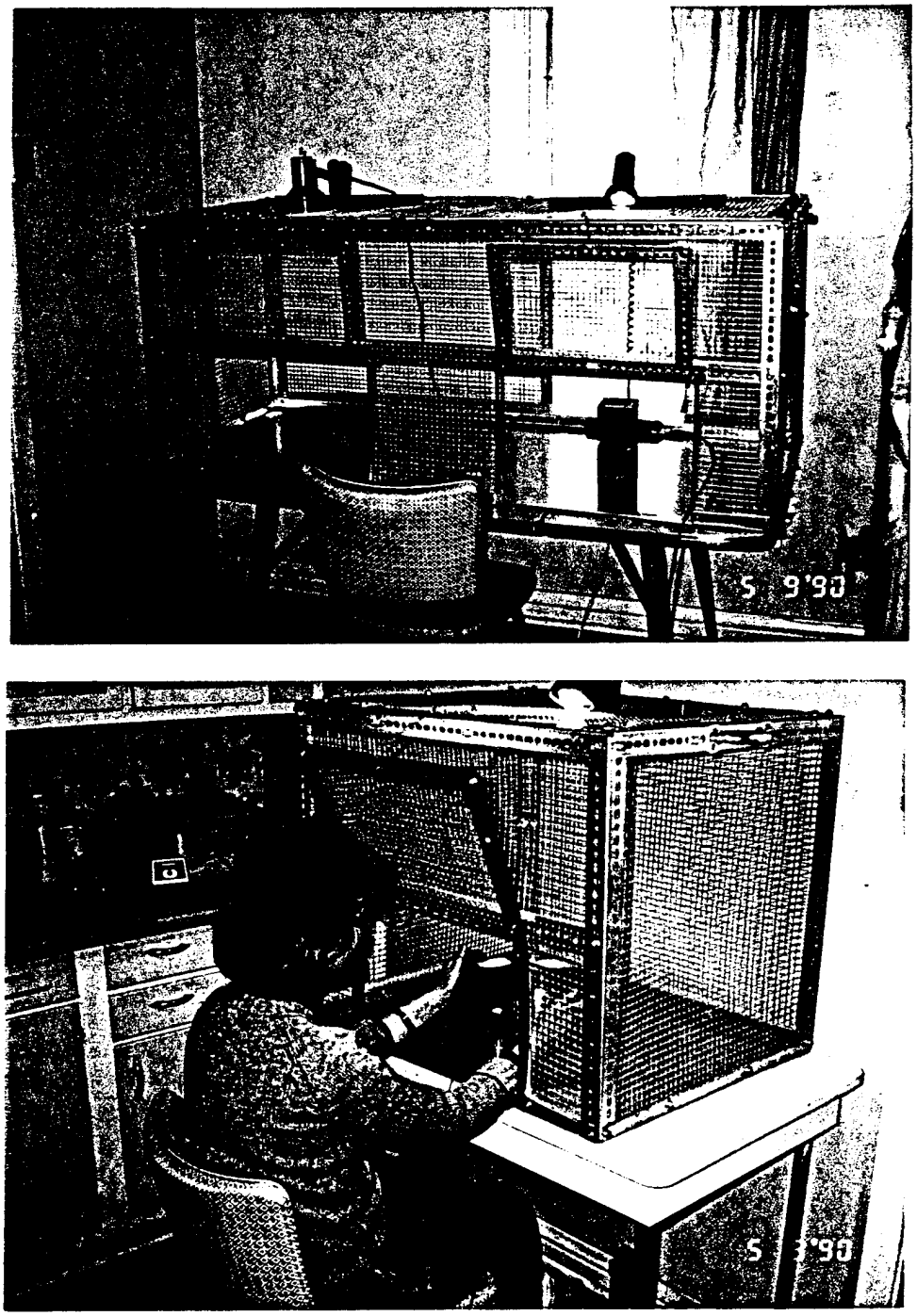


FIGURE 5a, b. Wire mesh Faraday cages, used to reduce exposure of nests to 60hz EM fields while nest architecture measurements are made in Crystal Falls.

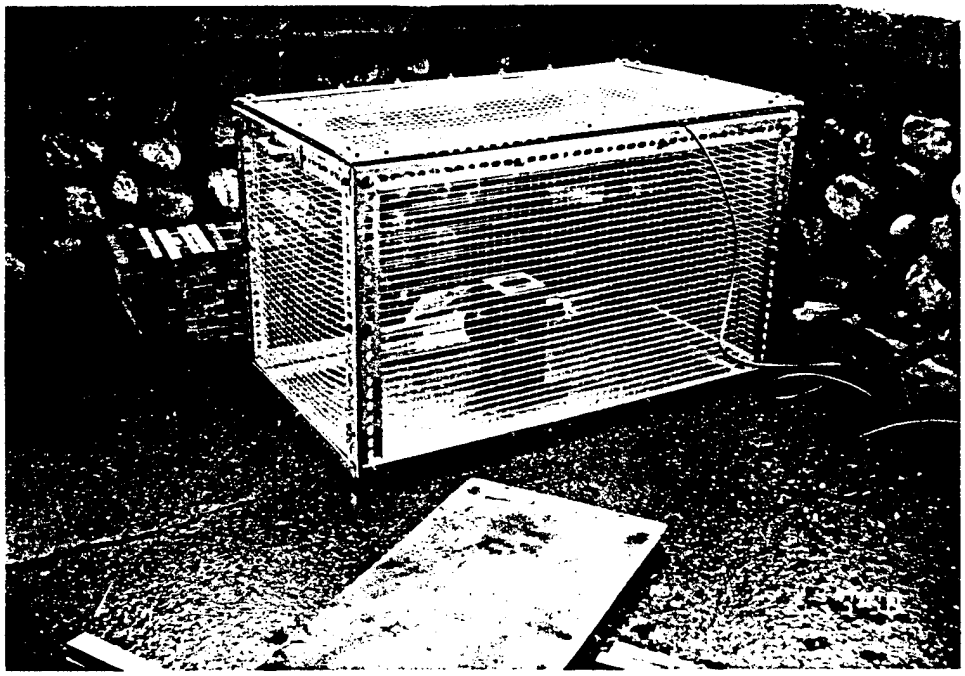


FIGURE 6. Wire mesh Faraday cage on front porch in Crystal Falls, used to store nests and cells just before and after nest measurements are made.

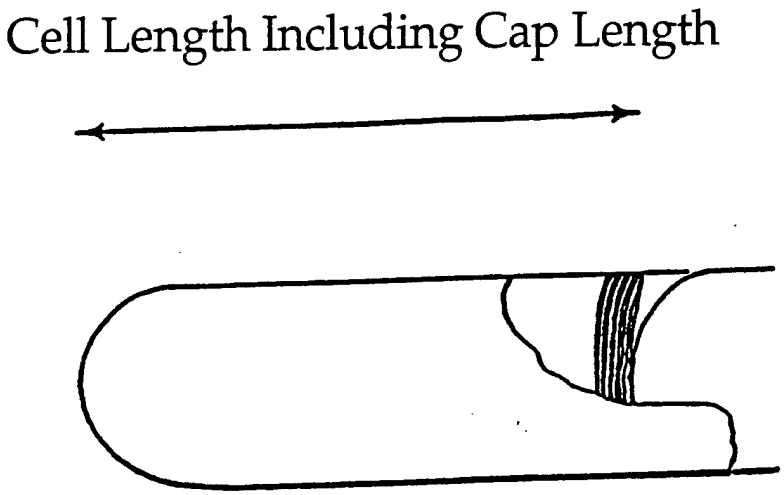


FIGURE 7. A single reproductive cell, indicating how cell lengths are measured.

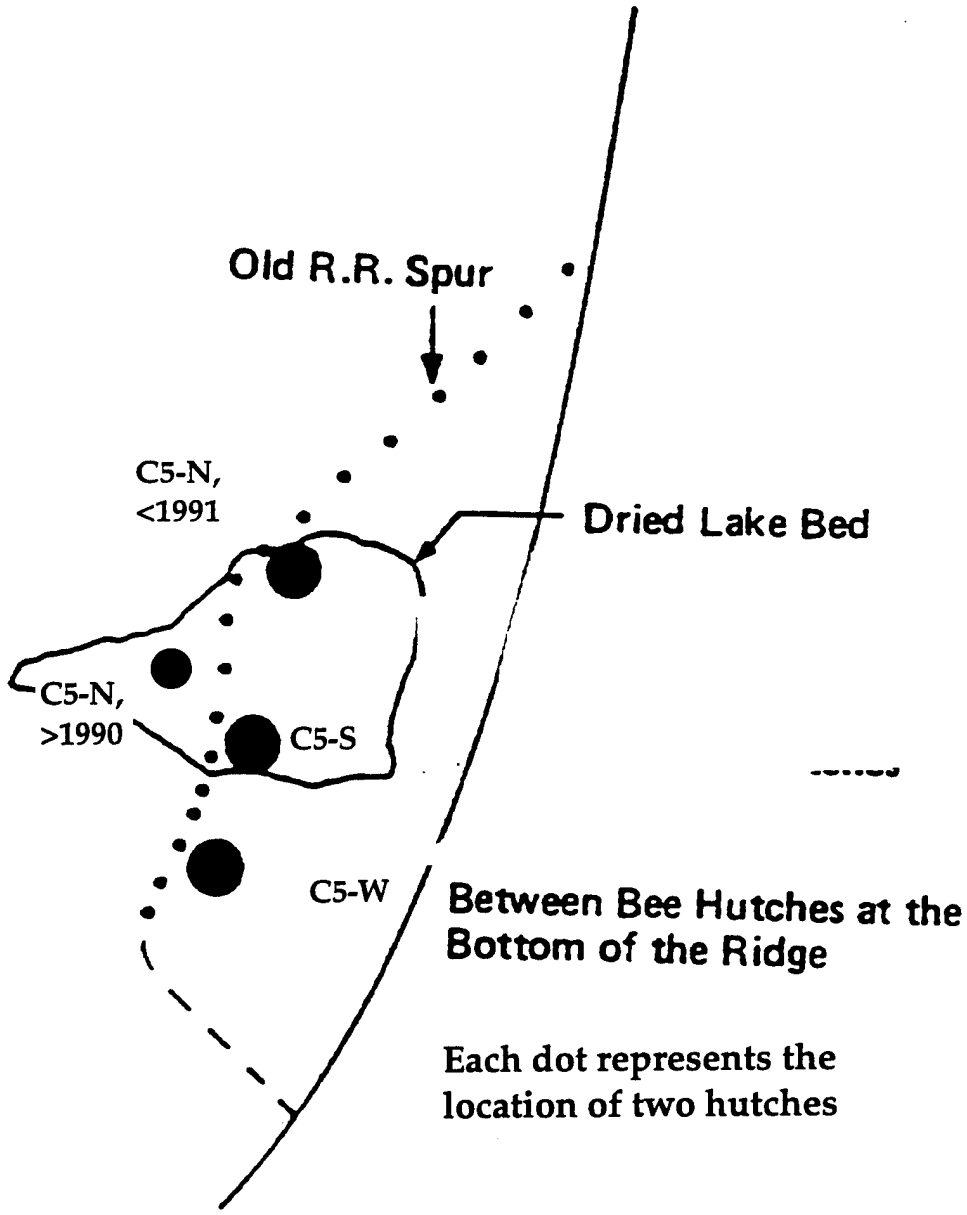


FIGURE 8. Schematic drawing of the C5 site and position of hutches.

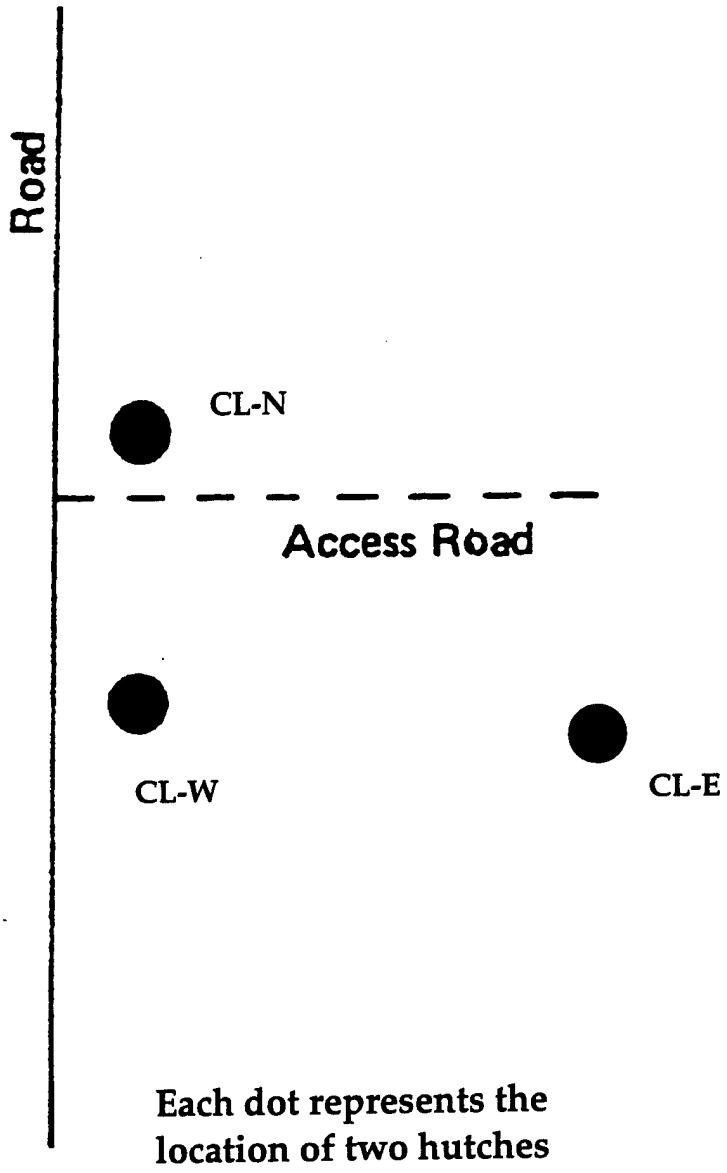


FIGURE 9. Schematic drawing of the CL site and position of hutches..

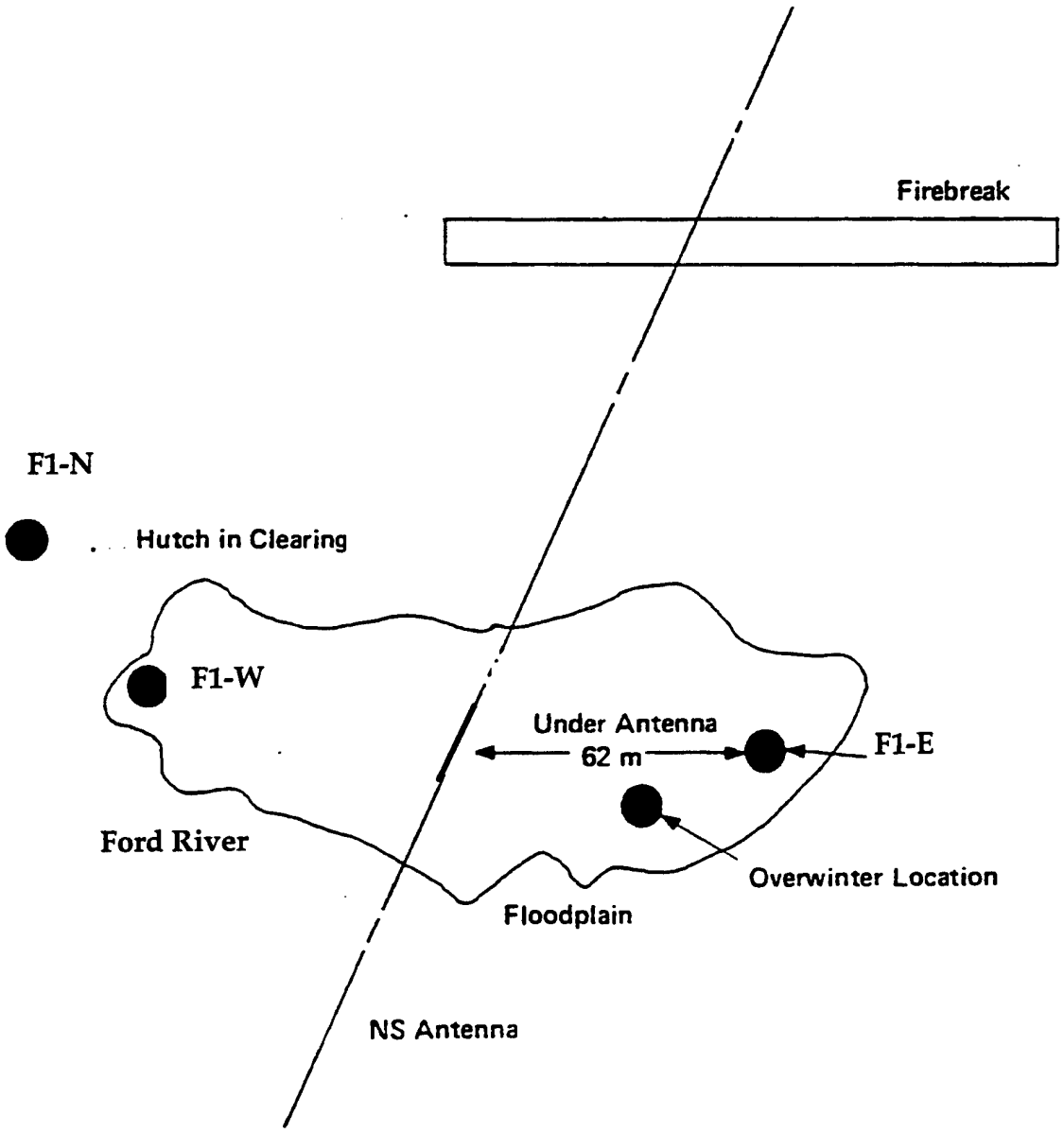


FIGURE 10. Schematic drawing of the F1 site and position of hutches.

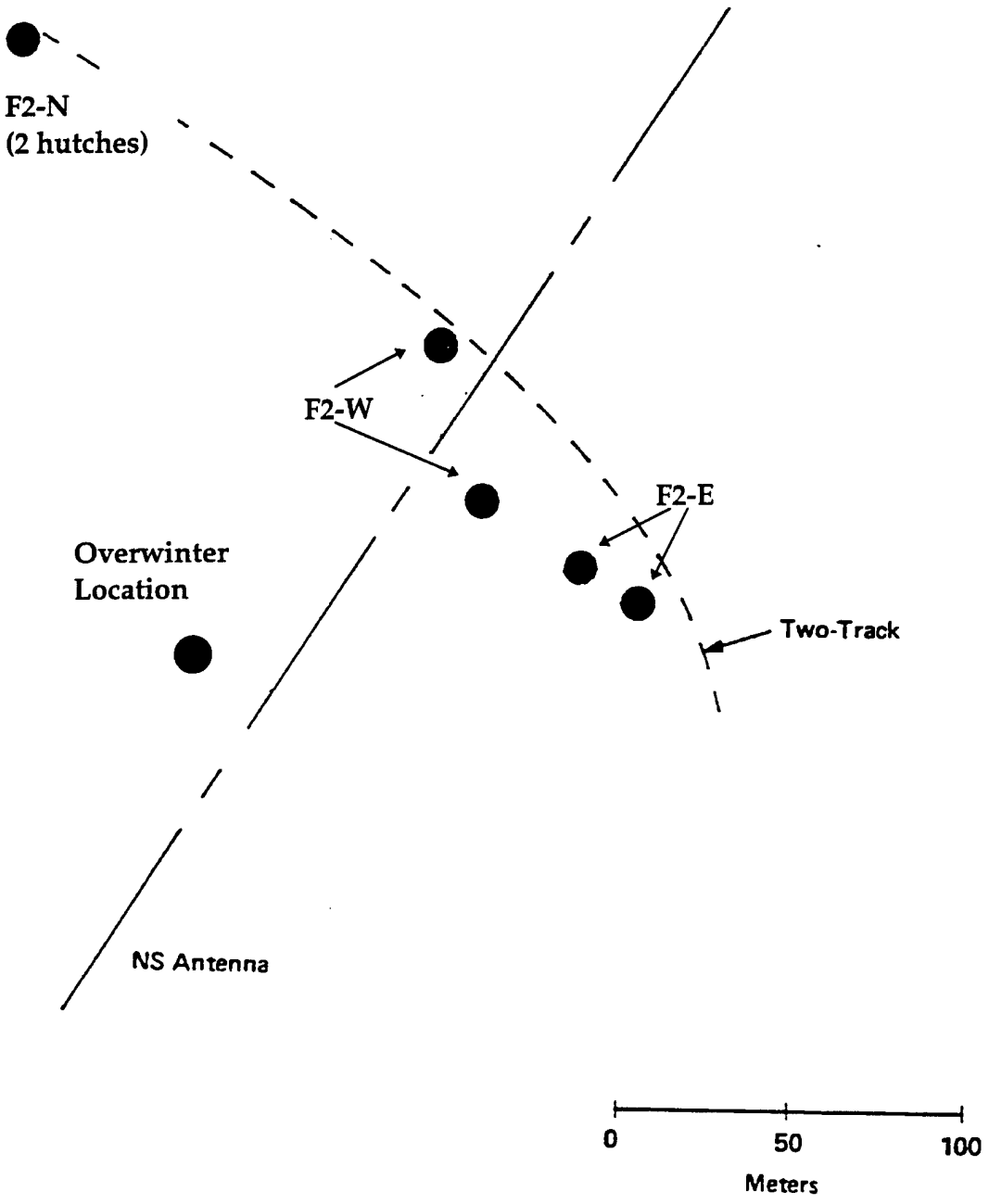


FIGURE 11. Schematic drawing of the F2 site and position of hutches.

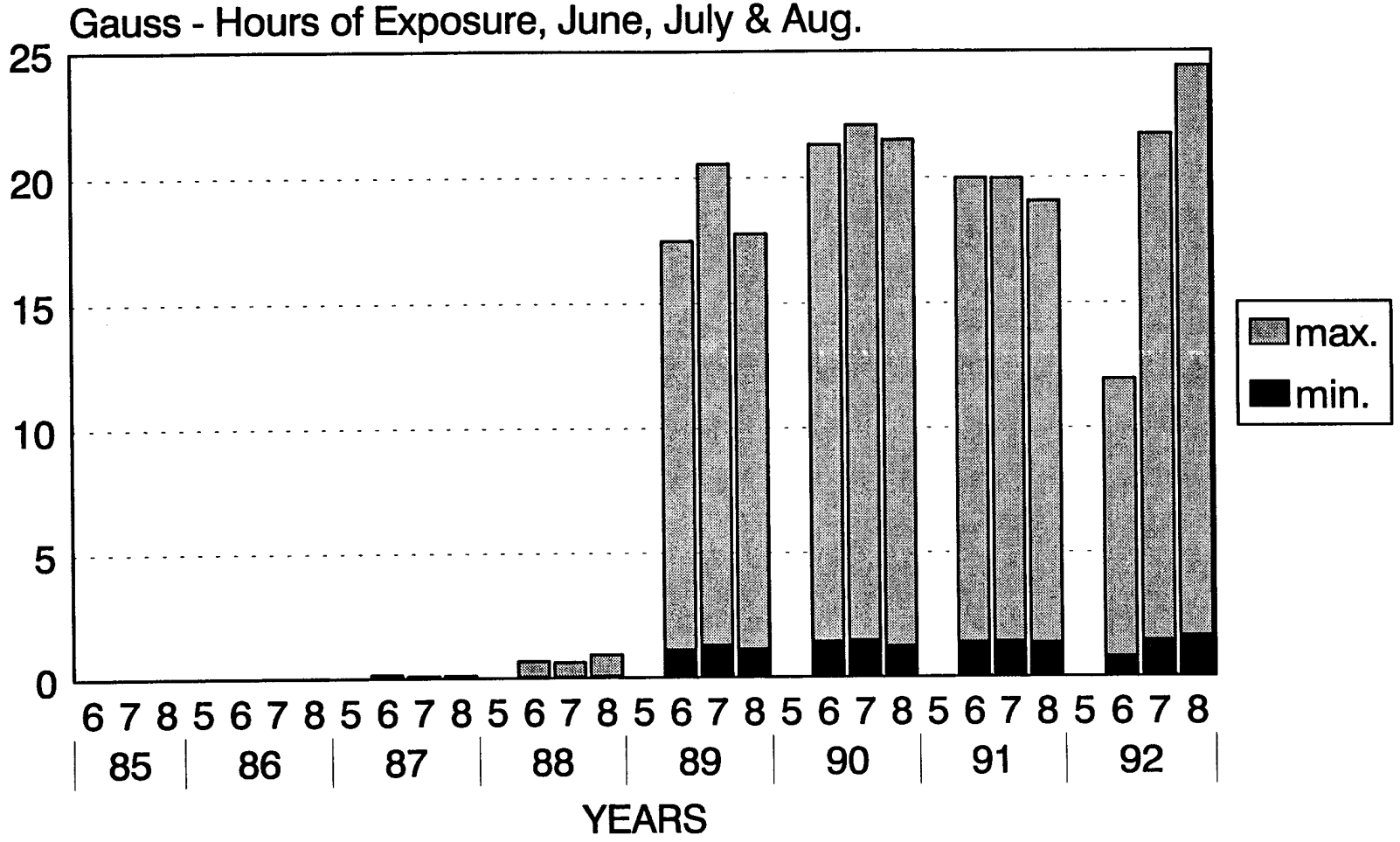


FIGURE 12. Cumulative magnetic field exposures (in Gauss-Hours) of foraging bees during the nesting season (June, July, August). A bee sitting directly under the antenna for the entire month would experience the maximum exposure plotted. A bee sitting on the hutch farthest from the antenna at the F2 site would experience the minimum exposure plotted. Most bees at the experimental sites would experience intermediate magnetic field exposures.

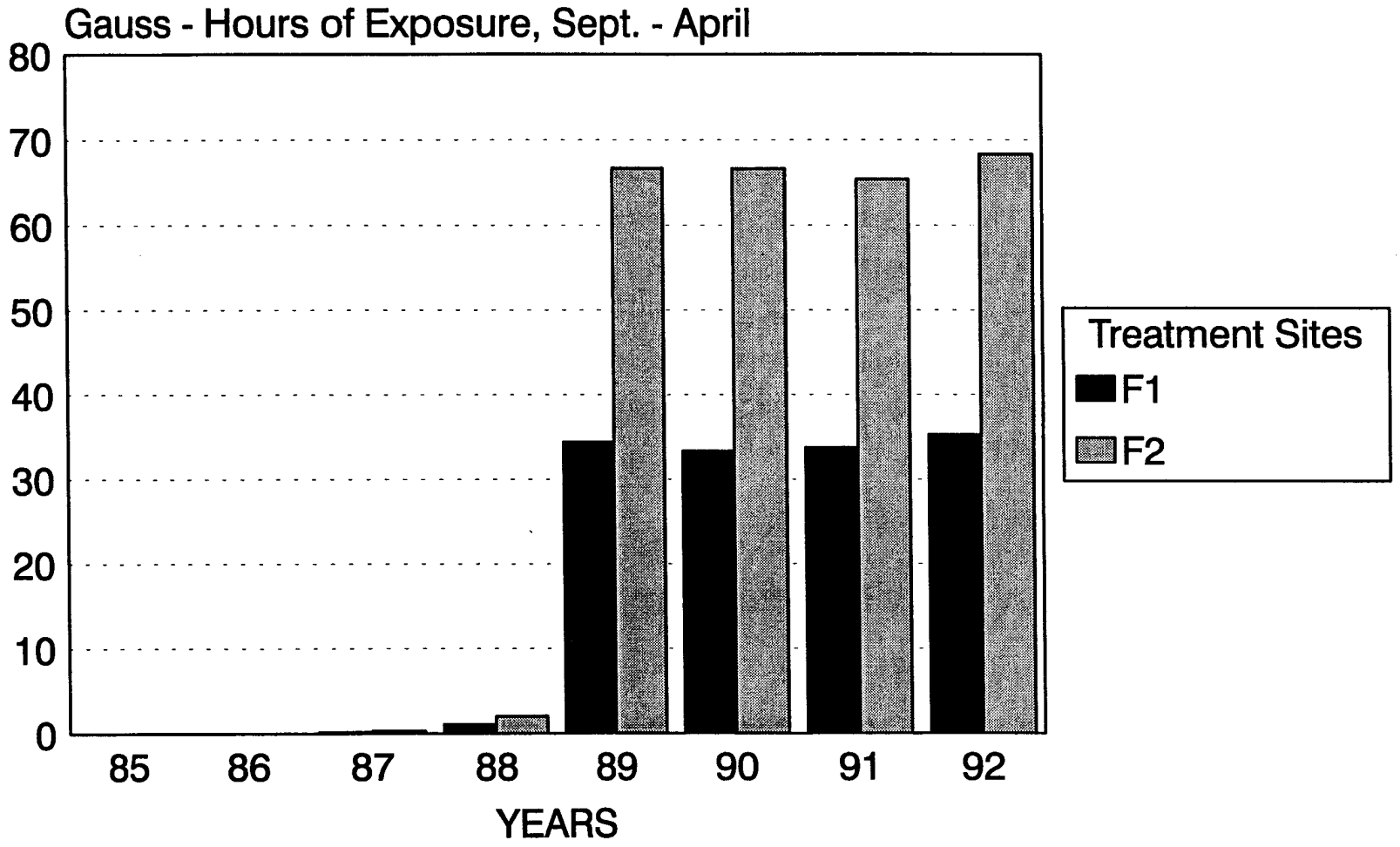


FIGURE 13. Cumulative magnetic field exposures (in Gauss-Hours) of overwintering prepupae between September and April.

TABLE 2. Basic form of the model used in GLM analyses. Degrees of freedom may differ for the two bee species. C represents constants calculated by SAS for each effect.

Source of Variation	Numerator df	Mixed Model F-Statistic
Exp (Fixed)	1	MS Exp / C* (MS Sites [Exp]) + C* (MS Error)
Sites[Exp] (Random)	2	MS Sites[Exp] / MS Error
Antenna (Fixed)	1	MS Antenna / C*(MS Yr[Antenna]) + C* (MS Measurer [Yr * Antenna]) + C* (MS Error)
Yr [Antenna] (Random)	3-6	MS Yr[Antenna] / C* (MS Measurer) [YR*Antenna]) + C* (MS Error)
Measurer[Yr*Antenna] Error (Random - Cell length and plug length analyses only)	12-15	MS Measurer [Yr*Antenna] / MS
Exp * Antenna	1	MS Exp * Antenna / MS Error
<u>Other fixed effects, tested in some models:</u>		
Expected Sex Early vs. Late Season Complete vs. Incomplete nests	1	MS Fixed Effect / MS Error
<u>Other covariates, tested in some models:</u>		
Diameter Cells per Nest Time^2	1	MS Covariate / MS Error

* 0.05 > P > 0.0011
** 0.001 > P > 0.00051
*** 0.0005 > P > 0.0001

TABLE 3. Number of nests of *M. relativa* which had at least one complete cell, by site. (Number of hutches with 5 or more nests.)

Year	Control Sites		Test Sites	
	C5	CL	F1	F2
		M. relativa		
1983	–	27	128	17
		(2)	(4)	(2)
1985	51	78	84	92
	(5)	(6)	(5)	(6)
1986	49	51	42	80
	(6)	(5)	(5)	(5)
1987	78	47	76	47
	(5)	(5)	(4)	(5)
1988	85	59	83	51
	(6)	(5)	(5)	(6)
1989	75	60	38	73
	(6)	(5)	(3)	(6)
1990	70	82	54	123
	(6)	(6)	(5)	(6)
1991	48	47	39	85
	(4)	(6)	(5)	(6)
1992	28	45	43	98
	(3)	(4)	(4)	(6)

TABLE 4. Number of nests of *M. inermis* which had at least one complete cell, by site. (Number of hutches with 5 or more nests.)

Year	Control Sites C5	Control Sites CL	Test Sites F1	Test Sites F2
		M. inermis		
1985				
nests measured	23	17	160	88
	(3)	(2)	(6)	(6)
nests constructed*	26	18	212	121
1986	15	2	40	65
	(1)	(0)	(3)	(4)
1987	56	25	122	108
	(3)	(3)	(5)	(6)
1988	30	7	54	127
	(3)	(0)	(2)	(5)
1989	106	23	172	262
	(6)	(3)	(6)	(6)
1990	163	51	237	382
	(6)	(3)	(6)	(6)
1991	138	54	187	374
	(5)	(5)	(6)	(6)
1992	51	32	125	159
	(4)	(2)	(6)	(6)

* Some 1985 nests were not measured because they were used in a study of diapause. I do not have these nests, nor do I have the data from the diapause study.

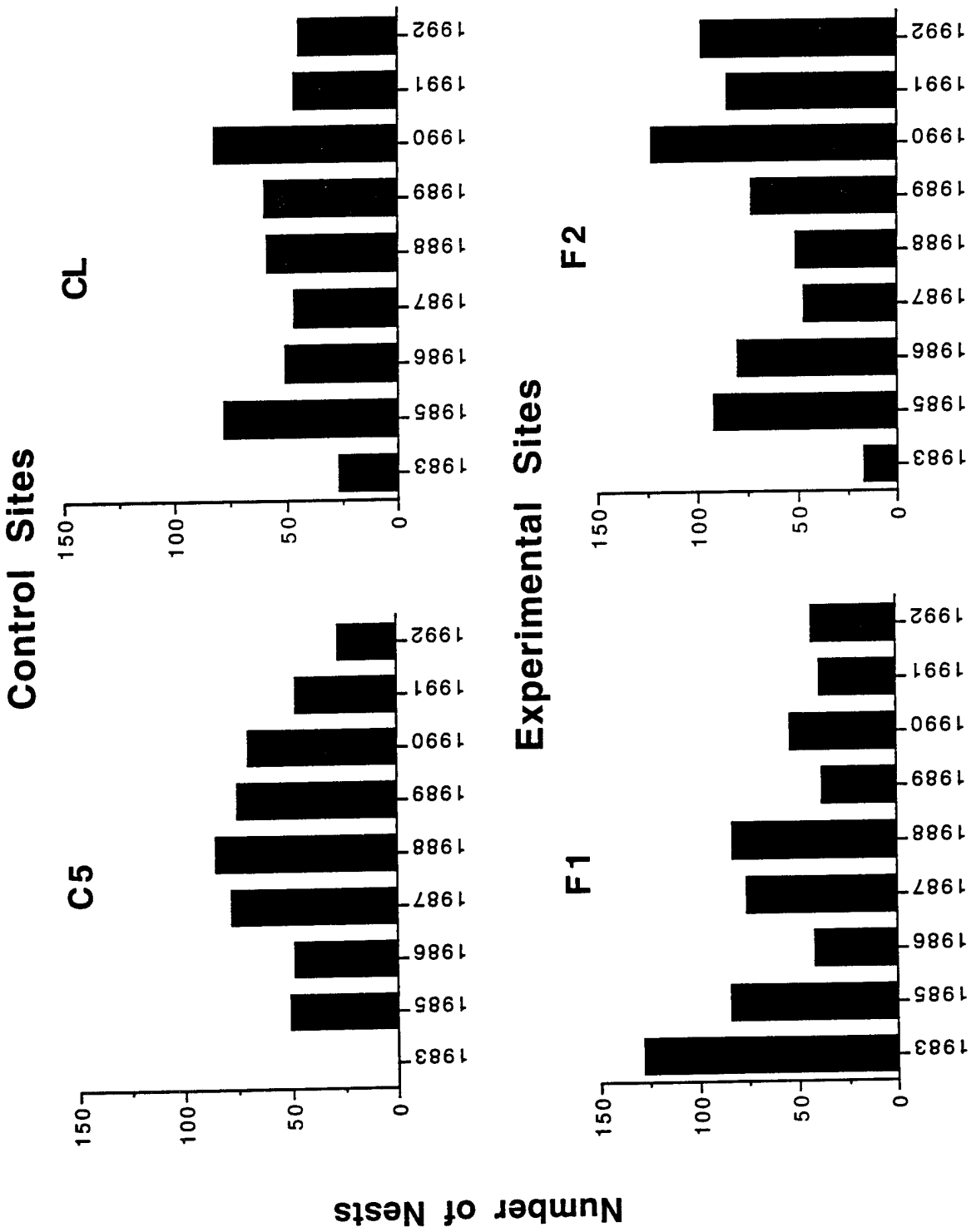


FIGURE 14. Number of nests of *M. relativa* with at least one complete cell, 1983-1992.

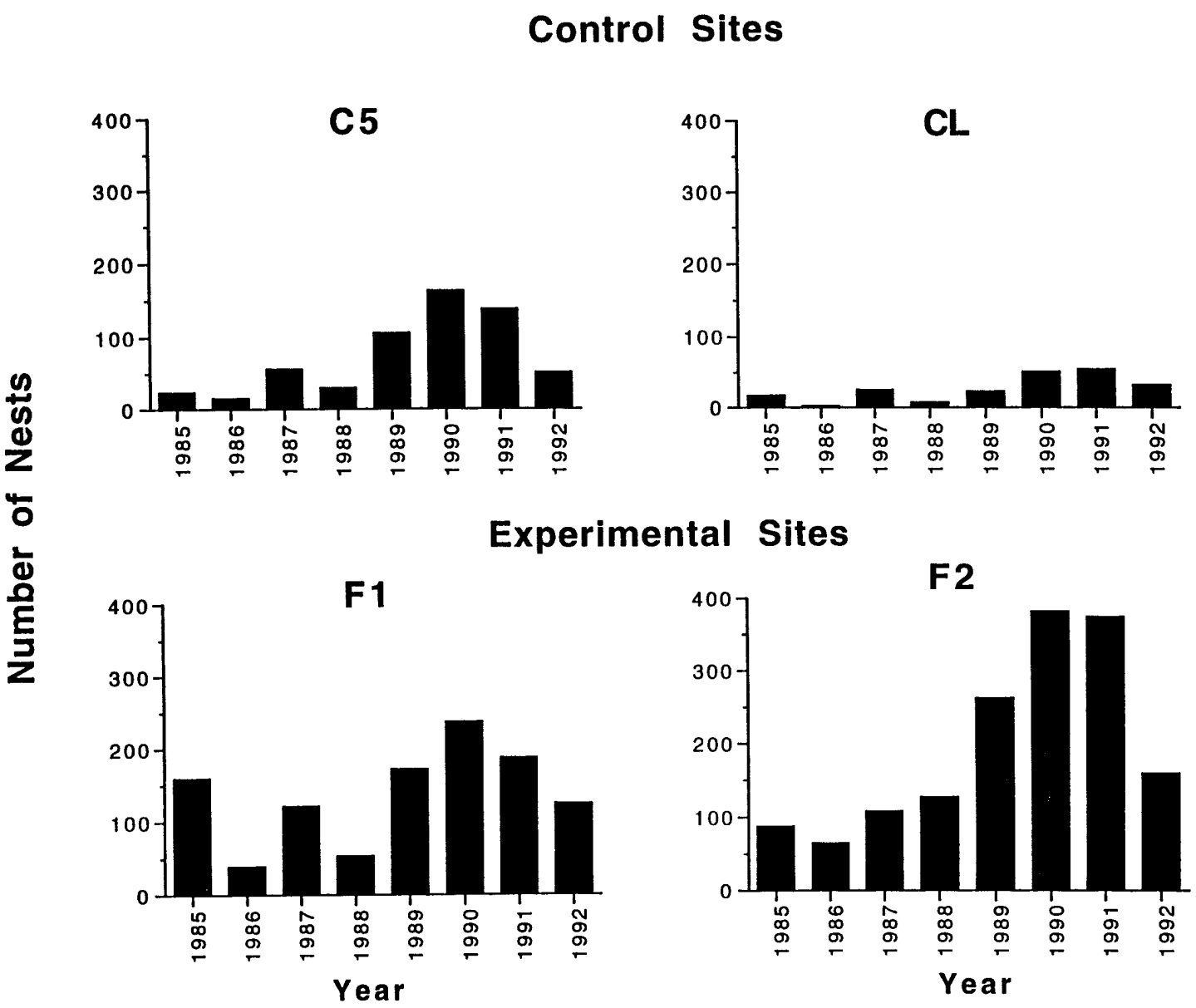


FIGURE 15. Number of nests of *M. inermis* with at least one complete cell, 1985-1992.

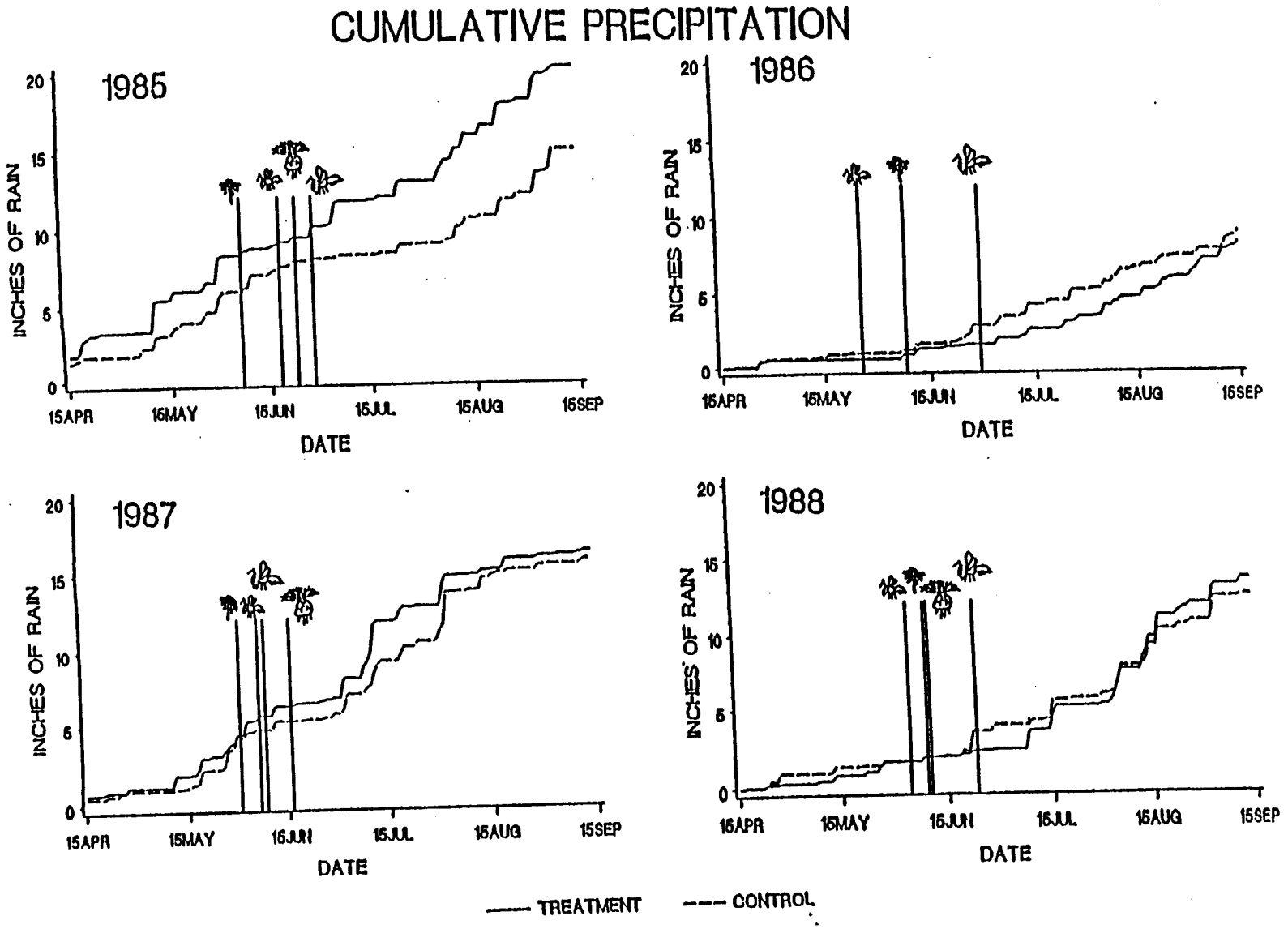


FIGURE 16. Cumulative precipitation at MTU pine plantations. Vertical lines indicate date of first nest of *M. relativa* (small bee) and *M. inermis* (large bee), and first bloom of orange hawkweed (*Hieracium aurantiacum*) and thistle (*Cirsium palustre*).

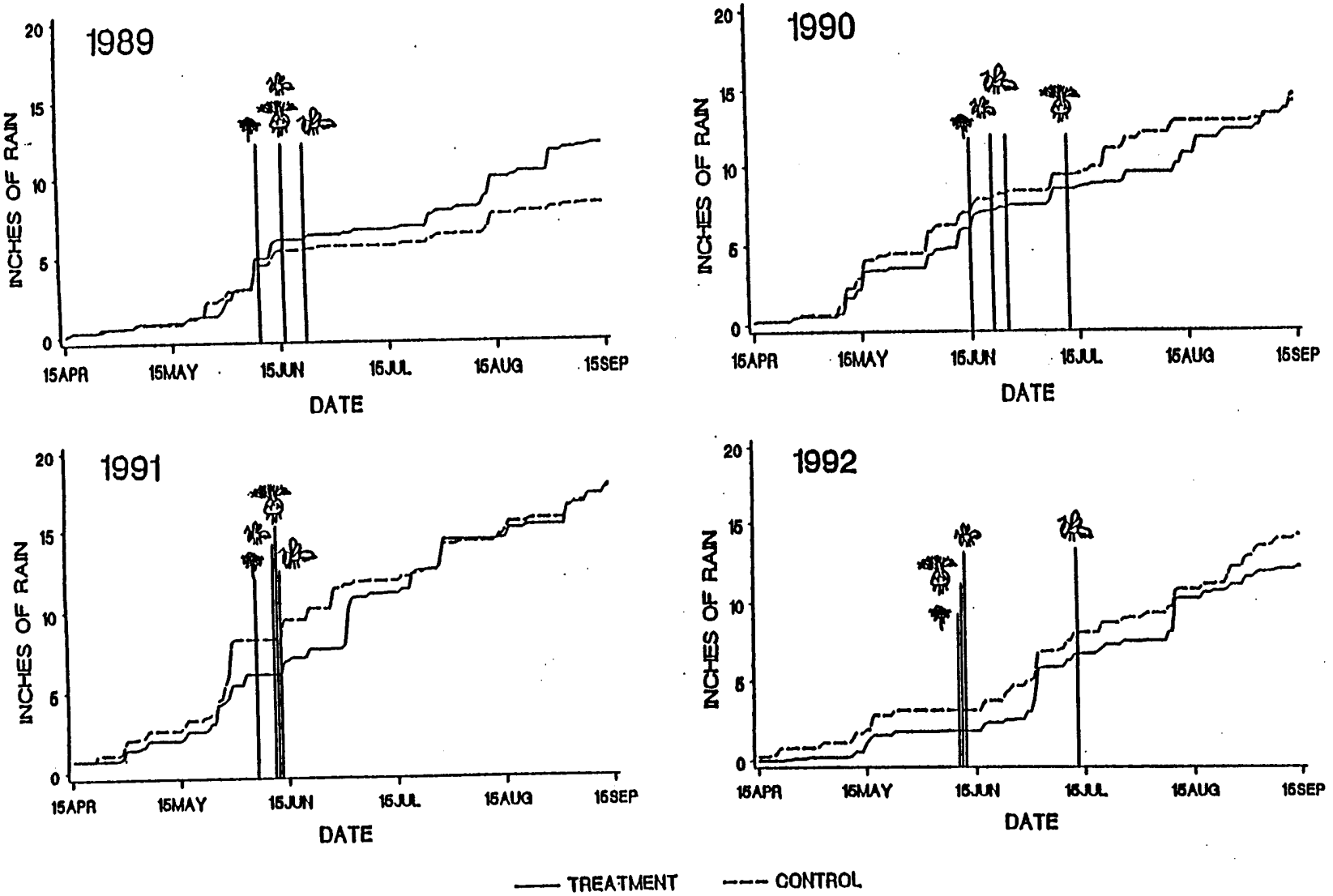


FIGURE 16 (cont.). Cumulative precipitation at MTU pine plantations.

TABLE 5. Date of first nest construction, and midpoint of the season.

Year	M. relativa		M. inermis	
	First nest	Median nest	First nest	Median nest
1983		7/16		
1985	6/18	7/19	6/28	8/12
1986	5/26	7/16	6/29	7/20
1987	6/6	7/4	6/8	7/16
1988	6/4	7/28	6/23	7/13
1989	6/16	7/18	6/22	7/25
1990	6/21	7/31	6/25	8/3
1991	6/11	7/5	6/13	7/8
1992	6/10	8/1	7/10	8/3

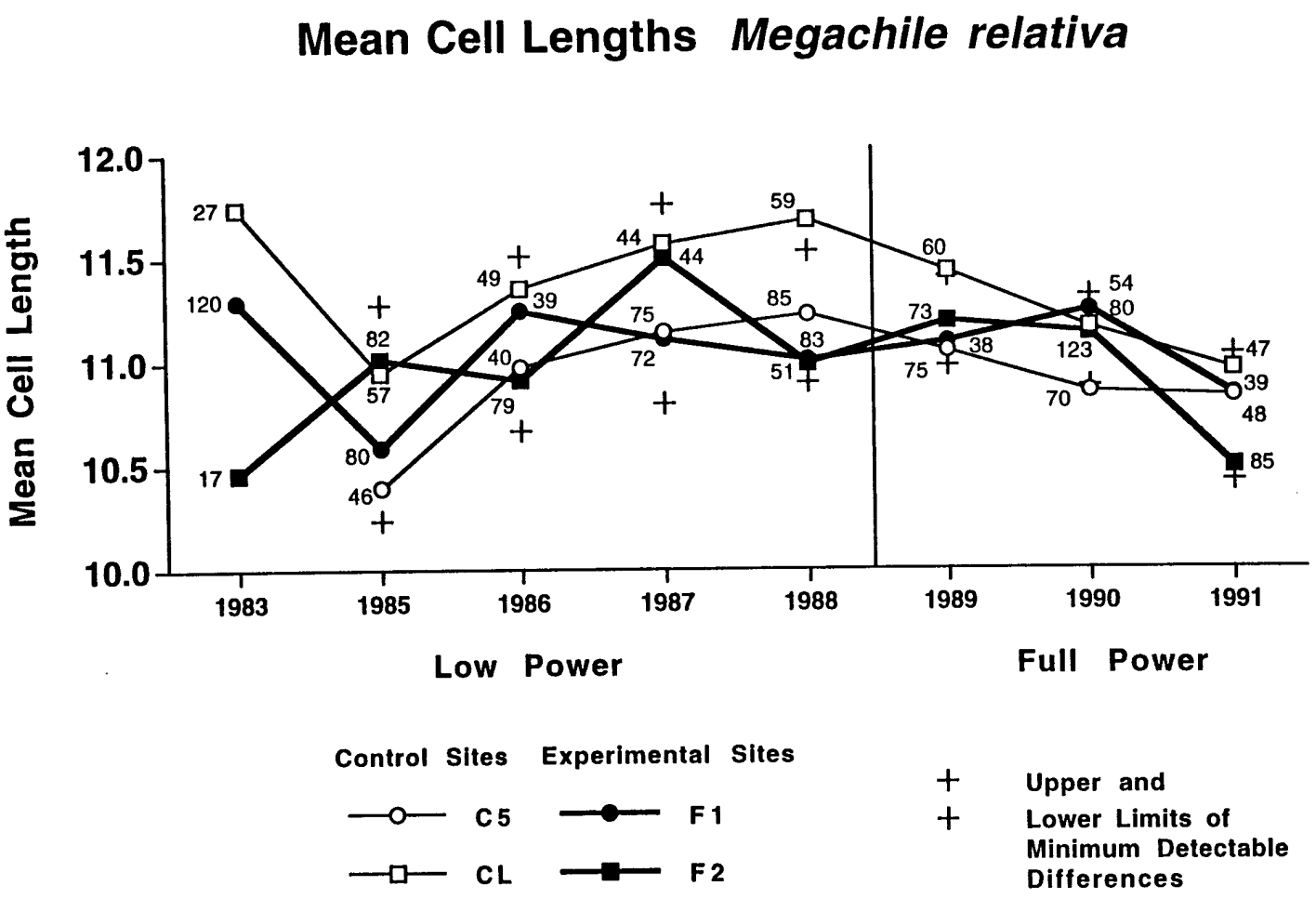


FIGURE 17. Mean cell length for *M. relativa* nests, 1983-1991, all cells. Numbers indicate sample sizes; + indicates the upper and lower limits to the minimum detectable difference between experimental and control sites for each year.

TABLE 6. GLM of mean cell length for all cells from 1983-1991 *M. relativa* nests.

CELL LENGTHS

Source of variation	Numerator df	MS	F	P>F
Exp	1	0.39	0.05	0.8436
Site [Exp]	2	7.83	10.86	0.0001***
Antenna	1	2.34	0.75	0.4102
Year [Antenna]	6	9.32	4.20	0.0079*
Measurer [Year * Antenna]	17	2.40	3.32	0.0001***
Exp * Antenna	1	3.62	5.02	0.0252*
Diameter	1	16.23	22.47	0.0001***
Complete vs. incomplete	1	5.53	7.66	0.0057*
Cells per nest	1	58.18	80.55	0.0001***
Early vs. Late Season	1	52.74	73.03	0.0001***
Model	32	268.57	11.62	0.0001***
Error	1908	1377.98		
$\bar{X}$ = 11.1 mm	CV=7.7	R^2=0.16	For α=0.05 Power of Exp * Antenna= 0.61	

TABLE 6 (continued)

Parameter	Estimates:	T for H_0: Parameter = 0	PR>|T|	$\bar{X}$	SE
Exp * Antenna					
Control Low	0.18	2.24	0.0252	11.19	0.09
Control Full	0.00	–	–	10.94	0.05
Experimen. Low	0.00	–	–	11.06	0.09
Experimental Full	0.00	–	–	11.00	0.05
Year (Antenna)					
Low: 1983	0.508	0.59	0.5524	11.39	0.40
1985	-0.467	-4.06	0.0001***	10.80	0.05
1986	-0.092	-0.57	0.5674	11.04	0.06
1987	0.198	1.77	0.0776	11.29	0.07
1988	0.0	–	–	11.12	0.06
Full: 1989	0.243	1.90	0.0571	11.19	0.06
1990	0.079	0.71	0.4753	11.02	0.05
1991	0.0	–	–	10.69	0.06
					SD
Site C5	0.0	–	–	11.32	0.94
CL	0.249	4.17	0.0001***	10.97	0.84
F1	0.111	1.96	0.0499*	11.06	0.92
F2	0.0	–	–	10.99	0.93
Diameter	-0.170	-4.74	0.0001***		
Complete vs.	0.129	2.77	0.0057**		
Incomplete	0.0	–	–		
Cells per nest	-0.082	-8.98	0.0001***		
Early Season vs.	0.349	8.55	0.0001***		
Late Season	0.0	–	–		

TABLE 7. GLM of mean cell length for 1983-1991 *M. relativa* nests; expected sex included in model.

CELL LENGTHS

Source of variation	Numerator df	MS	F	P>F
Exp	1	5.43	0.78	0.4671
Site [Exp]	2	8.68	13.79	0.0001***
Antenna	1	4.39	0.70	0.4354
Year [Antenna]	6	7.87	2.84	0.0491*
Measurer [Year * Antenna]	15	2.63	4.17	0.0001***
Exp * Antenna	1	4.05	6.43	0.0113*
Sex	1	118.99	188.99	0.0001***
Exp * Sex	1	0.59	0.93	0.3347
Antenna * Sex	1	2.22	3.53	0.0605
Exp * Antenna * Sex	1	1.64	2.61	0.1066
Diameter	1	24.48	38.88	0.0001***
Complete vs. incomplete	1	3.78	6.01	0.0143*
Cells per nest	1	37.04	58.83	0.0001***
Early vs. Late Season	1	37.55	59.63	0.0001***
Model	34	10.90	17.31	0.0001***
Error	1582	0.63		
$\bar{X}$ = 11.1 mm	CV=7.2	R^2=0.27	For α=0.05 Power of Exp * Antenna=0.72	

TABLE 7 (continued)

Parameter	Estimate:	T for H_0: Parameter = 0	PR> | T |	$\bar{X}$	SE
Exp * Antenna					
Control Low	0.096	0.98	0.3288	11.40	0.05
Control Full	0.0	–	–	11.11	0.06
Experimental Low	0.0	–	–	11.13	0.04
Experimental Full	0.0	–	–	11.10	0.05
Site [Exp]:					SD
C5	0.0	–	–	11.04	0.89
CL	0.30	4.64	0.0001***	11.38	0.93
F1	0.13	2.28	0.0228*	11.06	0.94
F2	0.0	–	–	10.93	0.88
Sex: Female	0.60	6.06	0.0001***	11.55	0.90
Male	0.00	–	–	10.90	0.87
Diameter	-0.22	-6.24	0.0001***		
Cells per nest	-0.07	-7.67	0.0001***		
Early Season vs.	0.33	7.72	0.0001***		
Late Season	0.0	–	–		

TABLE 8. Differences between measurers in mean cell lengths for *M. relativa*.

Measurer	Mean Cell Lengths mm	SD.	No. Nests Measured
JH (1983)	11.3	0.9	1
MA (1983)	11.3	0.7	162
VS (1983)	11.6	0.9	1
ER (1985)	10.8	0.1	85
ND (1985)	10.6	0.1	99
KS (1985)	11.0	0.1	81
JZ (1986)	11.2	0.1	64
KS (1986)	11.3	0.1	58
LS (1986)	10.7	0.1	49
MS (1986)	11.0	0.1	36
KS (1987)	11.3	0.1	99
LS (1987)	11.3	0.2	28
VS (1987)	11.3	0.1	108
BZ (1988)	10.9	0.1	68
KS (1988)	11.3	0.1	80
VS (1988)	11.1	0.1	130
BZ (1989)	11.1	0.1	79
KS (1989)	11.4	0.1	83
VS (1989)	11.1	0.1	84
JR (1990)	11.3	0.1	102
KS (1990)	10.8	0.1	72
VS (1990)	11.0	0.1	153
BZ (1991)	10.6	0.1	69
KS (1991)	10.6	0.1	55
VS (1991)	10.9	0.1	95

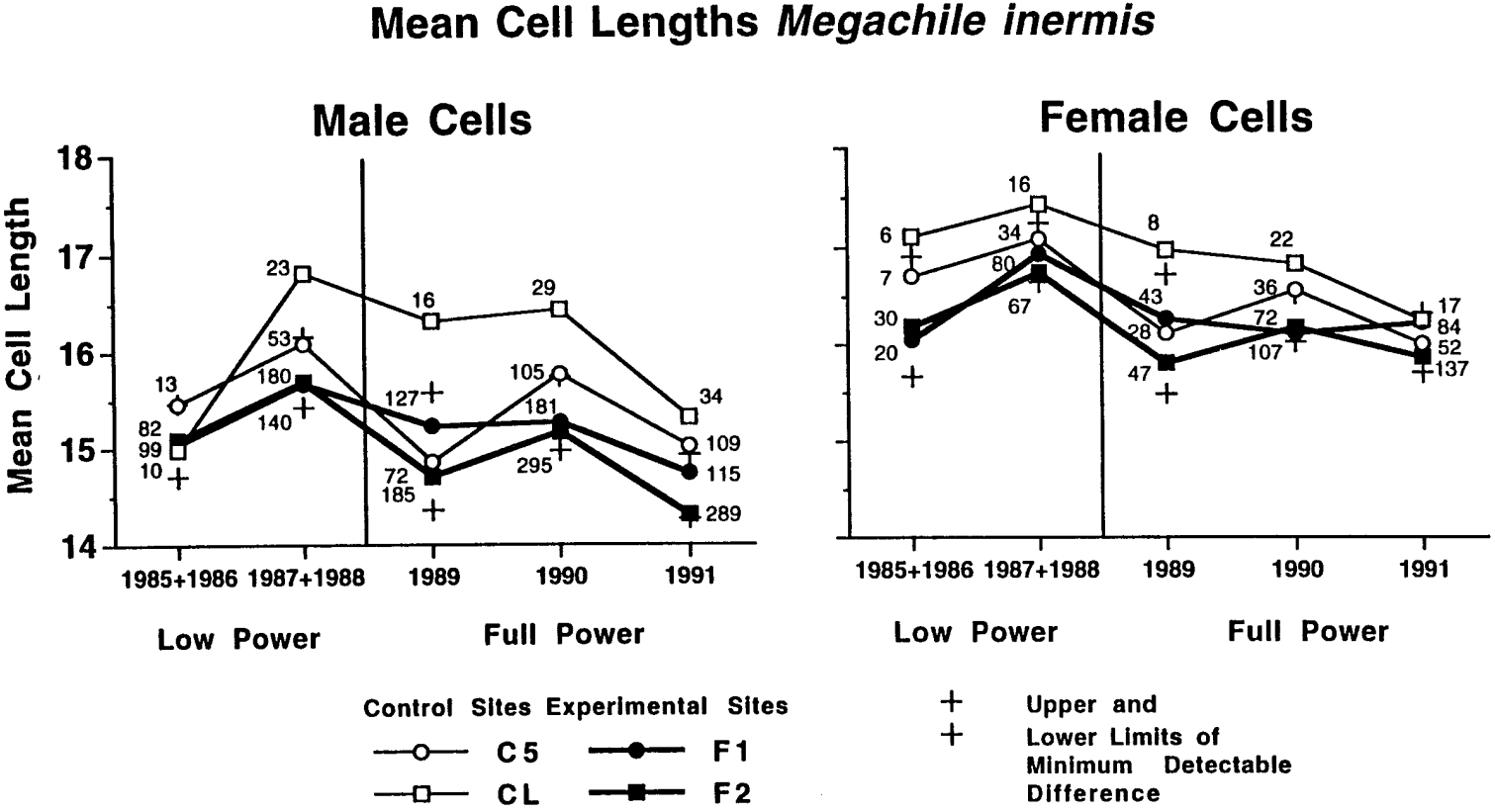


FIGURE 18. Mean cell length for *M. inermis* nests by sex; diameters >9.5mm. Numbers indicate sample sizes; + indicate upper and lower limits to the minimum detectable difference between experimental and control sites for each year.

TABLE 9. GLM of mean cell lengths for *M. inermis* nests; diameters > 9.5mm; expected sex included in the model.

CELL LENGTHS

Source of variation	Numerator df	MS	F	P>F
Exp	1	52.02	4.01	0.1731
Site [Exp]	2	27.40	28.32	0.0001***
Antenna	1	51.33	2.25	0.2468
Year [Antenna] 85+86, 87+88, 89, 90, 91	3	59.14	1.11	0.3823
Measurer [Year * Antenna]	12	57.85	59.79	0.0001***
Exp. * Antenna	1	0.37	0.39	0.5344
Sex	1	409.57	423.28	0.0001***
Exp. * Sex	1	3.70	3.82	0.0507
Antenna * Sex	1	0.06	0.06	0.8025
Exp * Antenna * Sex	1	0.06	0.07	0.7969
Diameter	1	6.80	7.03	0.0081*
Complete vs. incomplete	1	30.95	31.99	0.0001***
Cells per nest	1	277.95	287.26	0.0001***
Early vs. Late Season	1	5.08	5.25	0.0221*
Model	28	88.81	91.78	0.0***
Error	3041	0.97		
$\bar{X}$ = 15.5mm	CV = 6.3	R^2 = 0.46		

TABLE 9 (continued)

Parameter	Estimate	T for H_0: Parameter = 0	PR > |T|	$\bar{X}$	SD
Site [Exp]:					
C5	0.0	–	–	15.71	1.30
CL	0.475	5.51	0.0001***	16.35	1.35
F1	0.214	5.09	0.0001***	15.58	1.26
F2	0.0	–	–	15.26	1.32
Sex F	1.21	22.55	0.0001***	16.32	1.18
M	0.0	–	–	15.15	1.23
Diameter	0.11	2.65	0.0081*		
Complete vs.	0.380	5.66	0.0001***		
incomplete	0.0	–	–		
Season:					
Early vs.	0.097	2.29	0.0221*		
Late	0.0	–	–		

TABLE 10. Differences between observers in mean male cell lengths for *M. inermis*, bore diameters >9.5mm.

Measurer	Mean Cell Lengths mm	S.D.	No. Nests Measured
LS (1985-86)	15.0	1.1	138
MS (1985-86)	15.4	1.3	70
JZ (1985-86)	16.1	1.3	28
KS (1985-86)	16.5	1.2	31
LS (1987-88)	15.5	1.1	53
VS (1987-88)	15.8	1.1	286
BZ (1987-88)	15.8	1.1	34
KS (1987-88)	16.9	1.2	220
VS (1989)	15.1	1.1	260
BZ (1989)	14.7	1.3	137
KS (1989)	16.1	1.2	129
JR (1990)	15.7	1.1	284
KS (1990)	15.9	1.2	258
VS (1990)	15.3	1.1	305
BZ (1991)	14.4	1.3	311
KS (1991)	15.8	1.2	237
VS (1991)	15.2	1.1	289

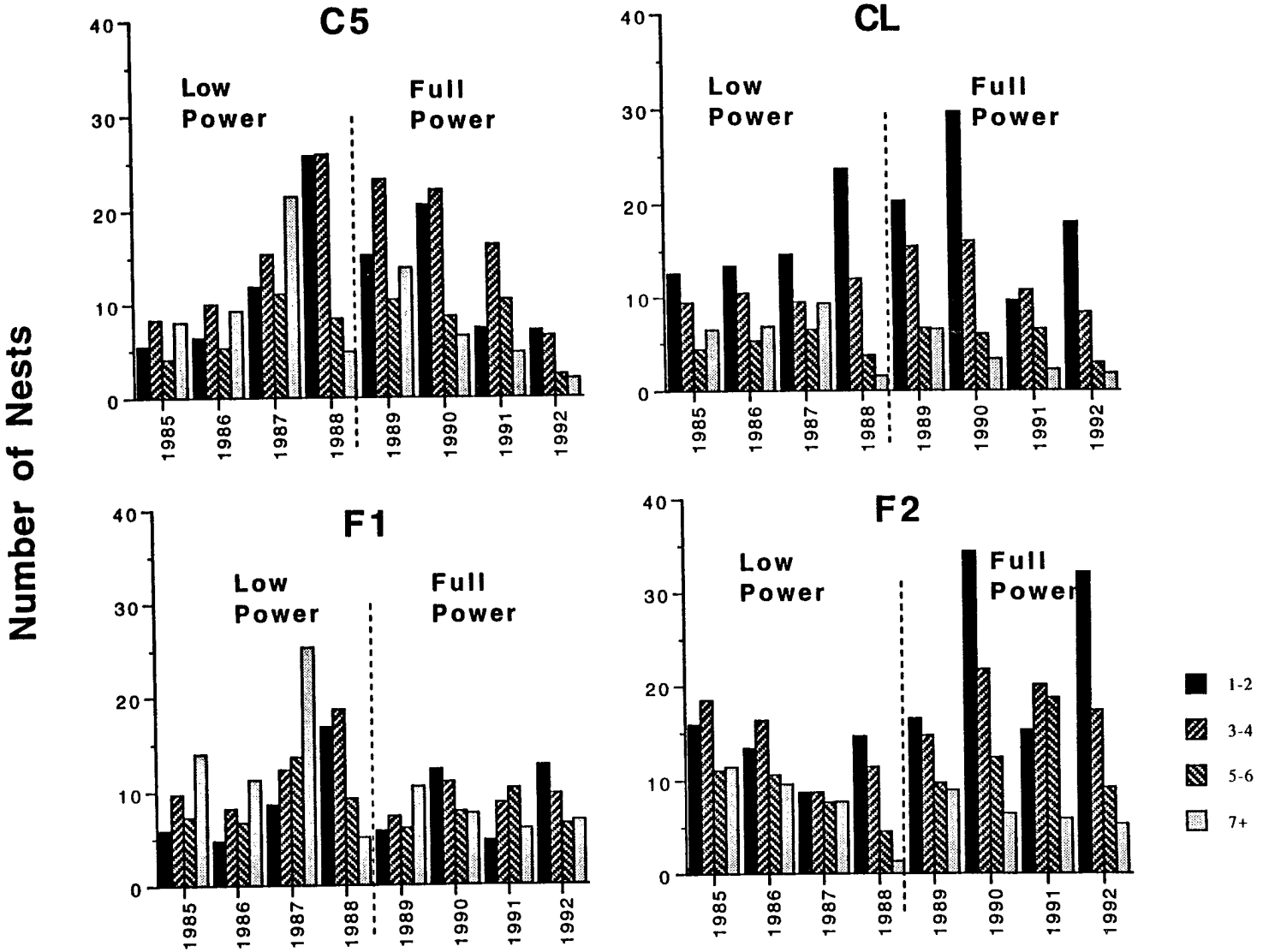


FIGURE 19. Predicted number of complete nests of *M. relativa* with 1-2, 3-4, 5-6 or 7+ cells.

TABLE 11. Categorical modeling analysis of number of cells per complete nest of *M. relativa*, 1985-1992.

NUMBER OF CELLS PER COMPLETE NEST

Source of variation	df	Chi.Square	Prob.
Intercept	3	49.23	0.0000***
Exp	3	13.63	0.0035*
Site[Exp]	6	33.89	0.0000***
Antenna	3	20.91	0.0001***
Year (Antenna)	18	79.99	0.0000***
Exp*Antenna	3	1.40	0.7057
Likelihood Ratio	60	82.02	0.0310*

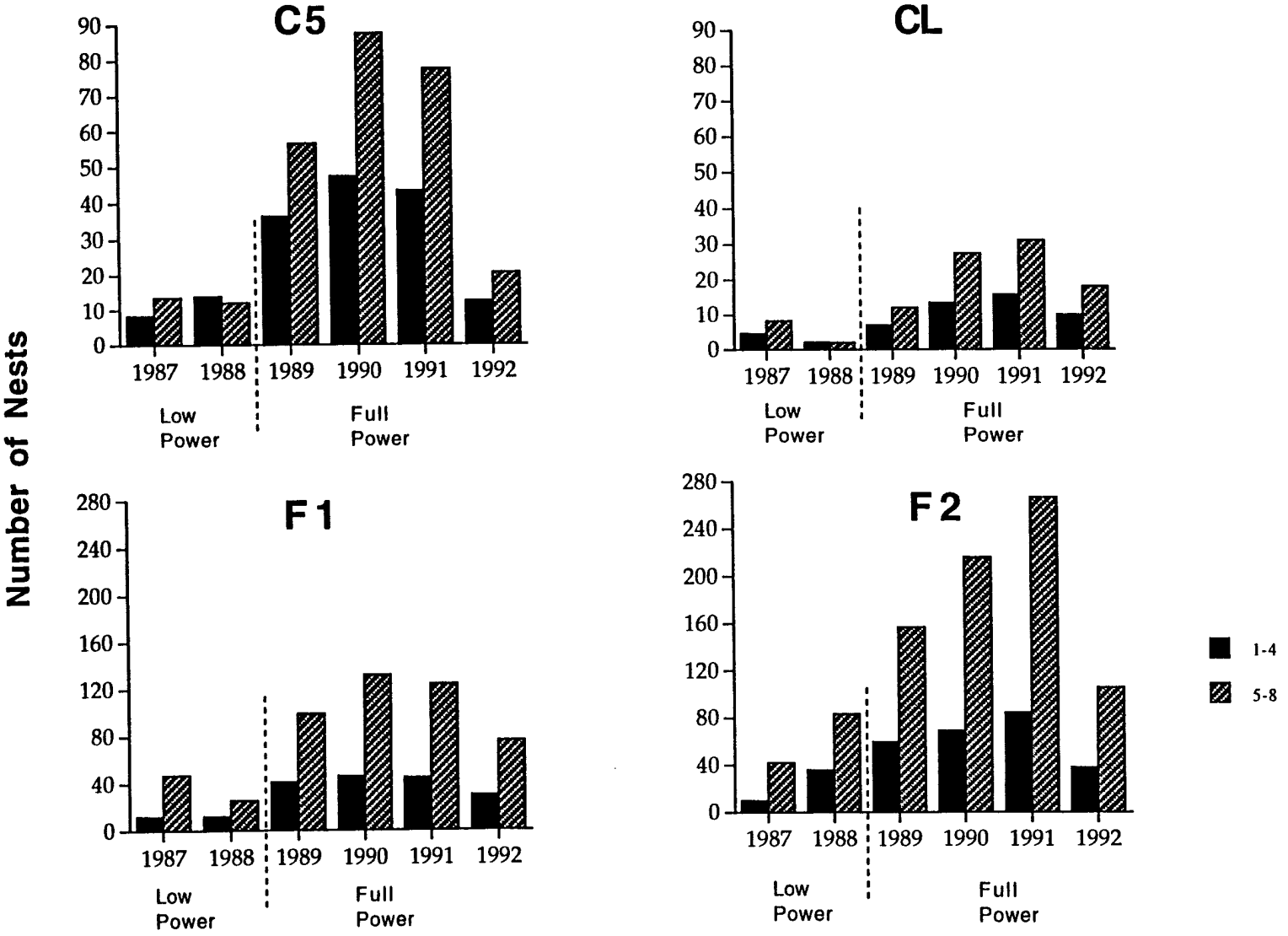


FIGURE 20. Predicted number of complete nests of *M. inermis* with few (1-4) or many (5-8) cells, diameters >9.5 mm, bore depths >135 mm.

TABLE 12. Categorical modeling analysis of number of cells per complete nest of *M. inermis*, 1987-1992: (diameters > 9.5mm, bore depths > 135mm).

NUMBER OF CELLS PER COMPLETE NEST

Source of variation	df	Chi.Square	Prob.
Intercept	1	30.10	0.0000***
Exp	1	14.97	0.0001***
Site[Exp]	2	1.34	0.5106
Antenna	1	5.67	0.0172*
Year (Antenna)	4	7.42	0.1152
Exp*Antenna	1	1.72	0.1892
Likelihood Ratio	14	32.35	0.0036*

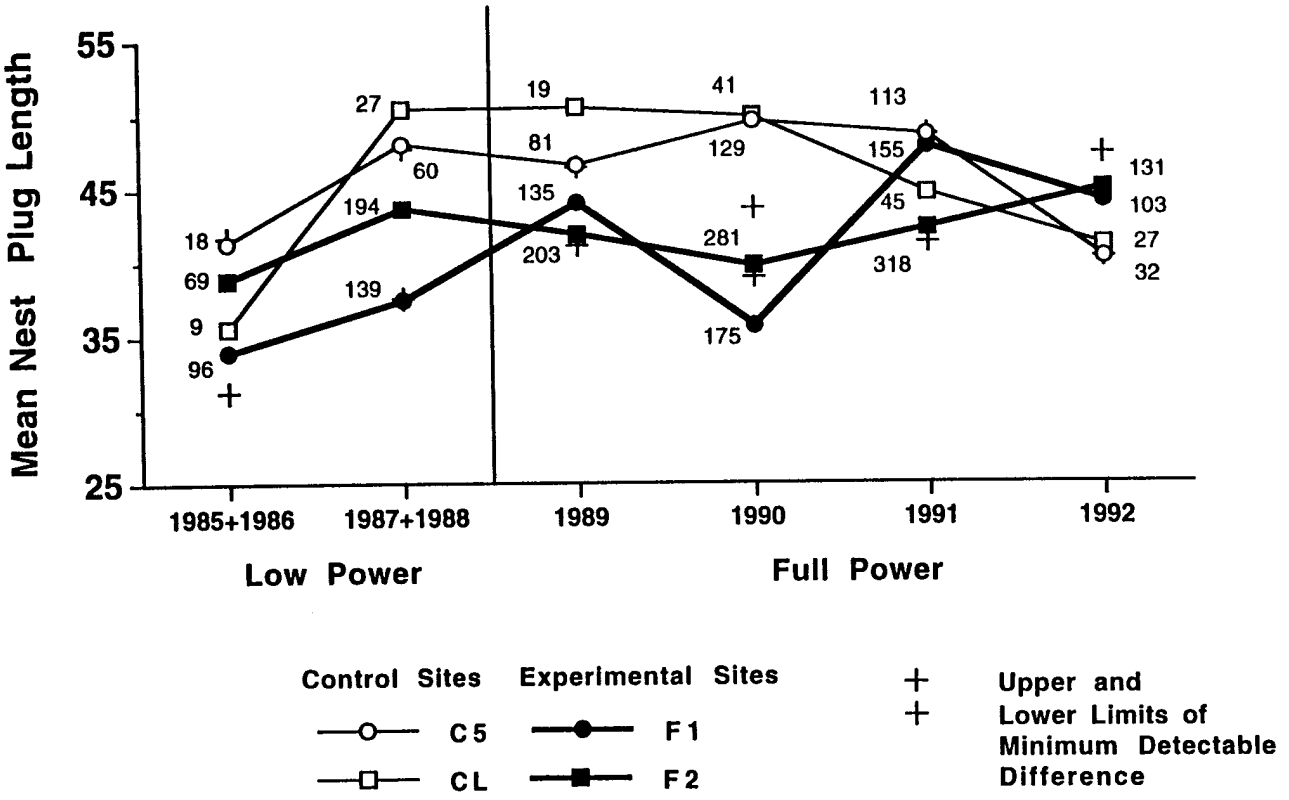


FIGURE 21. Mean nest plug lengths for *M. inermis*; diameters >9.5. Numbers indicate sample sizes; + indicate upper and lower limits to the minimum detectable difference between experimental and control sites for each year.

TABLE 13. GLM of *M. inermis* nest plug lengths from 1985-1992; diameters > 9.5mm.

PLUG LENGTHS

Source of variation	Numerator df	MS	F	P>F
Exp	1	2543.74	14.49	0.0004***
Site [Exp]	2	73.97	0.29	0.7504
Antenna	1	2318.02	1.29	0.3105
Year [Antenna] 85+86, 87+88, 89, 90, 91, 92	4	4064.78	11.37	0.0003***
Measurer [Year * Antenna]	13	359.31	1.40	0.1535
Exp * Antenna	1	315.67	1.23	0.2684
Diameter	1	2930.86	11.38	0.0008**
Cells per nest	1	187602.49	728.23	0.0001***
Early vs. Late Season	1	5431.77	21.09	0.0001***
Model	25	9647.33	37.45	0.0001***
Error	2574	257.62		
$\bar{X}$ = 42.79 mm	CV=37.51	R^2=0.27		

TABLE 13 (continued)

Parameter	Estimate:	T for H_0: Parameter = 0	PR> |T|	$\bar{X}$	SD
Exp:					
Control Sites	2.21	2.26	0.0241*	47.30	19.83
Experimental Sites	0.0	–	–	41.44	18.07
Year [Antenna]:					
Low: 85+86	-13.81	-5.19	0.0001***	36.47	17.61
87+88	0.0	–	–	42.69	17.52
Full: 89	5.70	2.96	0.0031*	43.83	19.36
90	0.30	0.17	0.8633	41.34	18.11
91	3.15	1.85	0.0640	45.02	18.70
92	0.0	–	–	43.85	19.78
Diameter	2.55	3.37	0.0008**		
Cells per nest	-6.94	-26.99	0.0001***		
Early Season vs. Late Season	3.38	4.59	0.0001***		
	0.0	–	–		

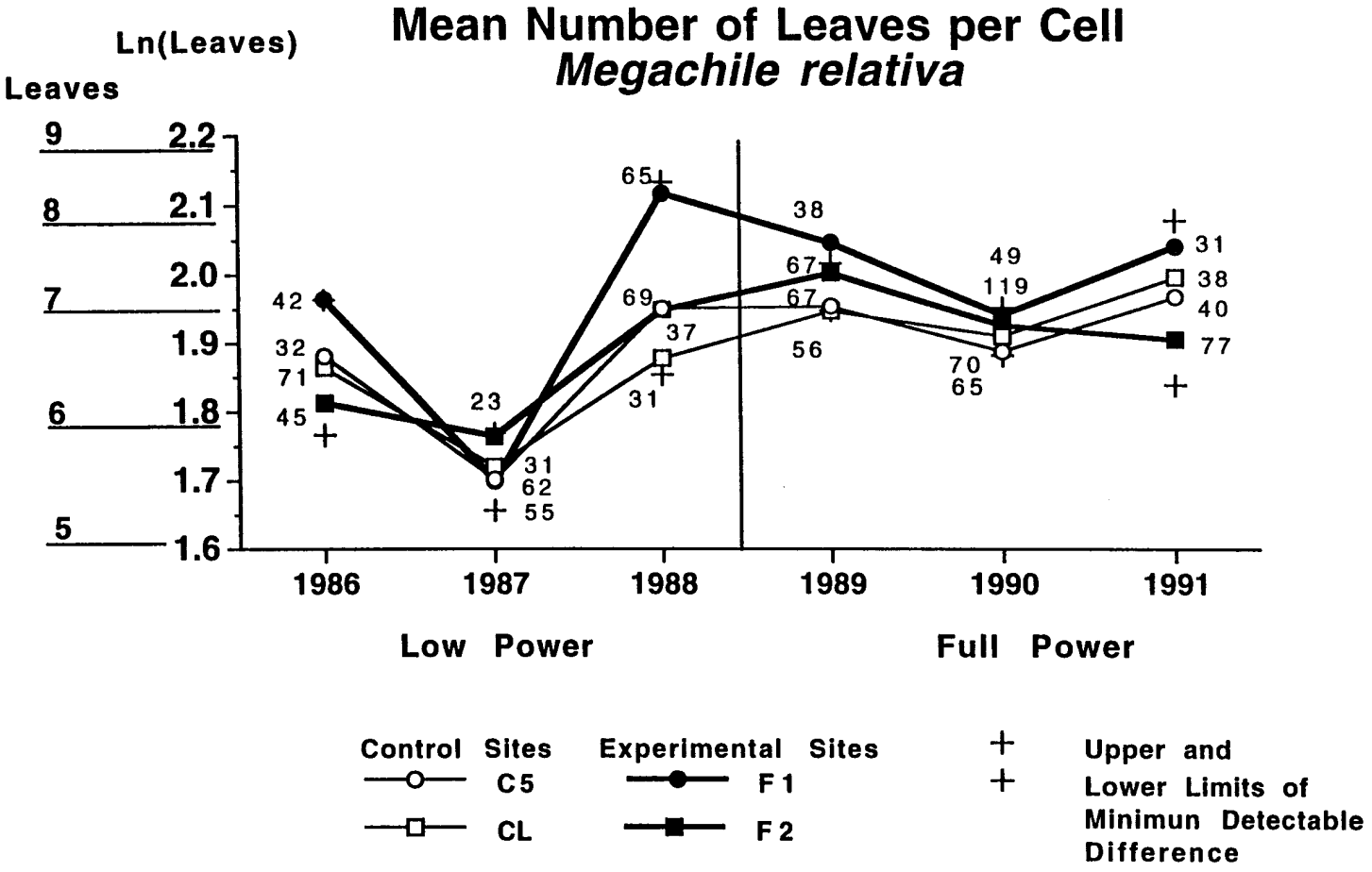


FIGURE 22. Mean leaves per cell for *M. relativa* nests. Numbers indicate sample sizes; + indicate the minimum detectable difference between experimental and control sites for each year.

TABLE 14. GLM of mean of leaves per cell for all cells from 1986-1992 *M. relativa* nests.

LEAVES PER CELL[1]

Source of variation	Numerator df	MS	F	P>F
Exp	1	0.60	1.65	0.3282
Site [Exp]	2	0.36	10.52	0.0001***
Antenna	1	0.70	0.63	0.4636
Year [Antenna]	5	1.24	36.01	0.0001***
Exp * Antenna	1	0.01	0.295	0.5873
Diameter	1	9.34	270.57	0.0001***
Complete vs. incomplete	1	0.09	2.57	0.1094
Cells per nest	1	0.05	1.58	0.2094
Early vs. Late Season	1	1.21	35.17	0.0001***
Model	14	1.57	45.38	0.0001***
Error	1394	0.03		
$\bar{X}$ = 1.91 (6.8 leaves)	CV=9.7	R^2=0.31		

[1] ln transformed

TABLE 14 (continued)

Parameter	Estimates:	T for H_0: Parameter = 0	PR>|T|	$\bar{X}$[1]	SE
Sites [Exp]					
C5	0.0	–	–	1.89	0.01
CL	0.001	0.01	0.9904	1.89	0.01
F1	0.067	4.58	0.0001***	1.97	0.01
F2	0.0	–	–	1.90	0.01
Year (Antenna)					
Low: 1986	-0.080	-4.12	0.0001***	1.91	0.01
1987	0.242	-12.14	0.0001***	1.75	0.01
1988	0.0	–	–	1.99	0.01
Full: 1989	0.093	4.44	0.0001	1.98	0.01
1990	-0.028	1.43	0.1535	1.92	0.01
1991	0.058	2.70	0.0071	1.95	0.01
1992	0.0	–	–		
Diameter	0.171	16.45	0.0001***		
Early Season vs. Late Season	-0.062	-5.93	0.0001***		
	0.0	–	–		

[1] Ln (Leaves per cell)

TABLE 15. GLM of mean of leaves per cell in *M. relativa* nests; expected sex included in the model.

LEAVES PER CELL[1]

Source of variation	Numerator df	MS	F	P>F
Exp	1	0.23	0.70	0.4872
Site [Exp]	2	0.45	13.21	0.0001***
Antenna	1	0.47	0.59	0.4773
Year [Antenna]	5	1.18	34.63	0.0001***
Exp * Antenna	1	0.06	1.81	0.1790
Sex	1	0.55	16.08	0.0001***
Exp * Sex	1	0.01	0.40	0.5259
Antenna * Sex	1	0.01	0.38	0.5377
Exp * Antenna * Sex	1	0.00	0.04	0.8452
Diameter	1	7.77	228.66	0.0001***
Complete vs. incomplete	1	0.01	0.18	0.6735
Cells per nest	1	0.01	0.19	0.6654
Early vs. Late Season	1	0.65	19.02	0.0001***
Model	18	1.07	31.64	0.0001***
Error	1122	0.03		
$\bar{X}$ = 1.90 (6.7 leaves)	CV = 9.7	R^2 = 0.34		

[1]ln transformed

TABLE 15 (continued)

Parameter	Estimate	T for H_0: Parameter = 0	PR > |T|	$\bar{X}^1$	SE
Sites [Exp]					
C5	0.0	–	–	1.87	0.01
CL	0.008	0.47	0.6390	1.88	0.02
F1	0.080	5.10	0.0001***	1.95	0.01
F2	0.0	–	–	1.87	0.01
Year [Antenna]					
Low 1986	-0.116	-5.22	0.0001***	1.88	0.02
1987	-0.270	-11.82	0.0001***	1.72	0.02
1988	0.0	–	–	1.99	0.02
Full 1989	-0.101	4.26	0.0001*	1.98	0.01
1990	-0.015	-0.68	0.4969	1.89	0.01
1991	0.048	2.03	0.0427	1.92	0.02
1992	0.0	–	–	1.88	0.02
Sex F	-0.041	-1.78	0.0755	1.86	0.13
M	0.0	–	–	1.92	0.01
Diameter	0.170	15.12	0.0001***		
Early vs.	-0.052	-4.36	0.0001***		
Late Season	0.0	–	–		

[1] Ln (Leaves per cell)

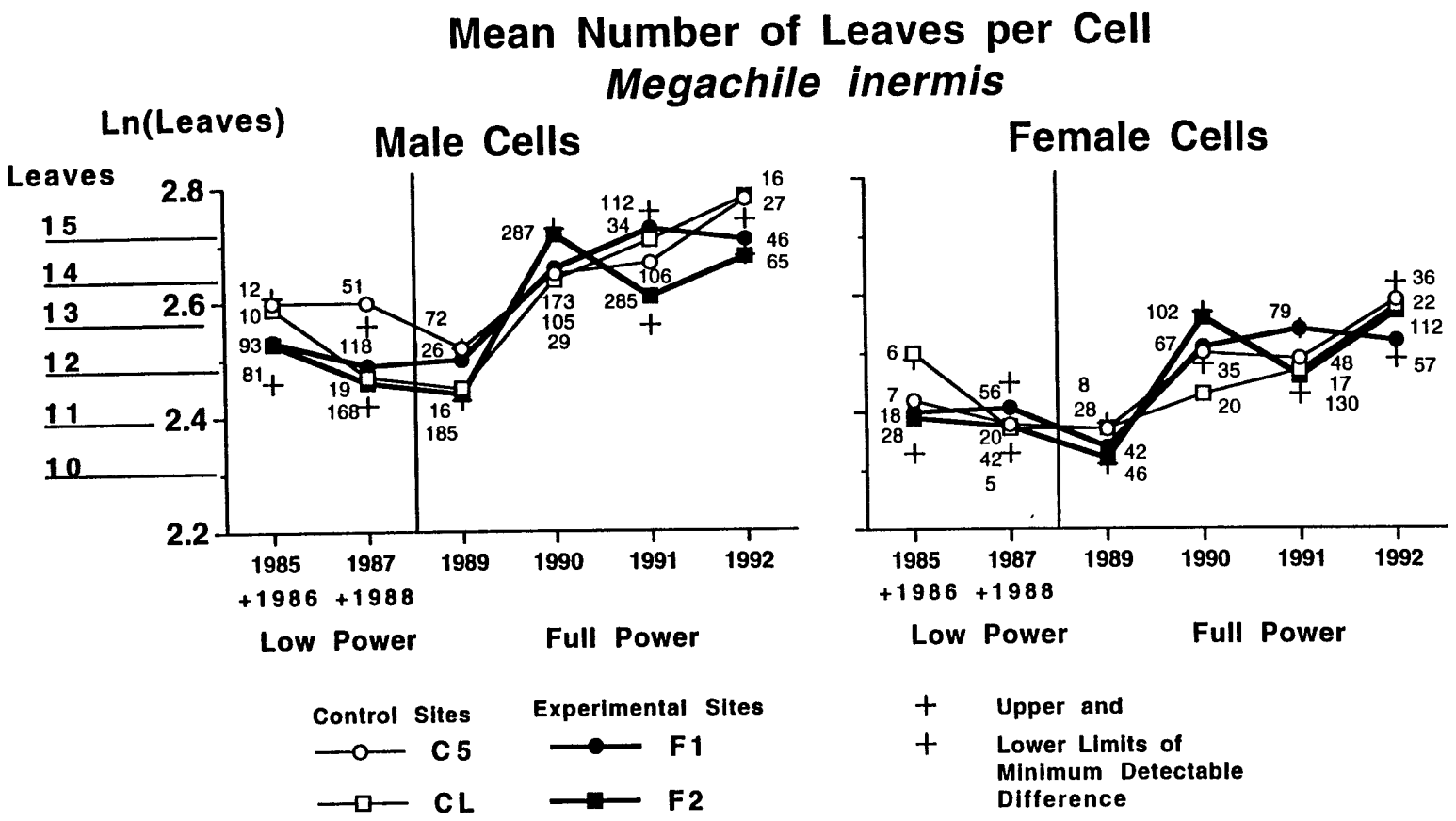


FIGURE 23. Mean leaves per cell for *M. inermis* nests by sex; diameters >9.5mm. Numbers indicate sample sizes; + indicate the minimum detectable difference between experimental and control sites for each year.

TABLE 16. GLM of mean of leaves per cell in *M. inermis* nests; diameters >9.5mm; expected sex included in the model.

LEAVES PER CELL[1]

Source of variation	Numerator df	MS	F	P>F
Exp	1	0.28	5.11	0.0739
Site [Exp]	2	0.10	3.24	0.0395*
Antenna	1	0.05	0.12	0.7466
Year [Antenna] 85+86, 87+88, 89, 90, 91, 92	4	1.11	35.66	0.0001***
Exp * Antenna	1	0.17	5.57	0.0183*
Sex	1	5.90	188.62	0.0001***
Exp * Sex	1	0.13	4.25	0.0394*
Antenna * Sex	1	0.05	1.46	0.2265
Exp * Antenna * Sex	1	0.04	1.42	0.2341
Diameter	1	13.18	421.63	0.0001***
Complete vs. incomplete	1	0.33	10.65	0.0011*
Cells per nest	1	0.19	6.21	0.0127**
Early vs. Late Season	1	5.05	161.63	0.0001***
Model	17	3.35	107.19	0.0001***
Error	3253	0.03		
$\bar{X}$ = 2.56 (12.8 leaves)	CV = 6.9	R^2 = 0.36	For α=0.05 Power of Exp * Antenna=0.65	

[1]ln transformed

TABLE 16 (continued)

Parameter	Estimate	T for H_0: Parameter = 0	PR > |T|	$\bar{X}^1$	SD
Exp * Antenna					
Control Low	0.074	3.31	0.0010**	2.58	0.02
Control Full	0.0	–	–	2.57	0.01
Experimental Low	0.0	–	–	2.52	0.01
Experimental Full	0.0	–	–	2.56	0.01
Sites [Exp]					
C5	0.0	–	–	2.58	0.01
CL	-0.013	-0.89	0.3736	2.57	0.02
F1	0.017	2.39	0.0171*	2.55	0.01
F2	0.0	–	–	2.54	0.01
Year [Antenna]					
Low 1985 + 1986	0.032	2.25	0.0243*	2.57	0.01
1987 + 1988	0.0	–	–	2.54	0.01
On 1989	-0.047	-3.13	0.0017*	2.52	0.01
1990	0.062	5.21	0.0001***	2.63	0.01
1991	-0.018	-1.61	0.1061	2.55	0.01
1992	0.0	–	–	2.57	0.01
Sex F	-0.148	-16.53	0.0001***	2.49	0.01
M	0.0	–	–	2.63	0.01
Diameter	0.150	20.53	0.0001***		
Complete vs. In-complete	-0.038	-3.26	0.0011**		
	0.0	–	–		
Cells per nest	-0.007	-2.49	0.0127*		
Early vs. Late Season	-0.093	-12.71	0.0001***		
	0.0	–	–		

[1] ln (Leaves per cell)

TABLE 17. Log-likelihood ratio contingency tables for *M. relativa* nest entrance
H_0: Nest orientations at each hutch set are homogeneous between years (i.e., have the same directional preference).

	EW	NS	R			EW	NS	R	
		C5-S					CL-E		
1983	–	–	–			14	9	23	
1985	6	5	11			15	9	24	
1986	4	6	10	G=9.171		8	3	11	G=5.515
1987	6	16	22	df = 7		12	6	18	df=8
1988	4	19	23	n.s.		13	2	15	n.s.
1989	9	12	21			12	7	19	
1990	12	18	30			13	10	23	
1991	3	13	16			4	2	6	
1992	2	7	9			12	4	16	
C	46	96	142			103	52	155	
		C5-N					CL-N		
1983	–	–	–			–	–	–	
1985	4	2	6			12	7	19	
1986	5	6	11	G=6.623		10	7	17	G=8.620
1987	4	3	7	df=5		10	3	13	df=7
1988	12	3	15	n.s.		17	4	21	n.s.
1989	9	13	22			11	1	12	
1990	10	8	18			10	1	11	
1991	1	4	5*			7	2	9	
1992	2	1	3*			7	1	8	
C	44	35	79			84	26	110	
		C5-W					CL-W		
1983	–	–	–			–	–	–	
1985	8	14	22			7	4	11	
1986	11	7	18			6	8	14	
1987	18	18	36	G=11.270		5	6	11	G=4.001
1988	14	24	38	df=7		3	6	9	df=7
1989	14	10	24	n.s.		9	11	20	n.s.
1990	8	6	14			12	14	26	
1991	16	6	22			9	6	15	
1992	4	6	10			4	8	12	
C	93	91	184			55	63	118	
	C5 - BY HUTCH SETS					CL - BY HUTCH SETS			
C5-S	46	96	142		CL-E	103	52	155	
C5-N	44	35	79*	G=15.277[1]	CL-N	84	26	110	G=22.873[1]
C5-W	93	91	184	df=2	CL-W	55	63	118	df=2
C	183	222	405	P<.001		242	141	383	P<.001

1. Within hutch sets, data are homogeneous between years. However, hutch sets (data pooled across years) are heterogeneous. Thus, hutch set data cannot be pooled by year.
2. Within hutch sets data are heterogeneous; cannot be pooled.

orientation by hutch set and year.

H_1: Nest orientations at each hutch set are heterogeneous between years and hutch sets at a site, so data cannot be pooled.

EW	NS	R		EW	NS	R	
	F1-E				F2-E		
42	25	67		–	–	–	
15	6	21		9	5	14	
12	4	16	$G=6.393^2$	10	16	26	$G=12.428^1$
18	21	39	df=8	6	9	15	df=7
7	9	16	P<.04	4	16	20	n.s.
5	6	11		10	12	22	
5	7	12		6	20	26	
5	4	9		8	17	25	
1	7	8		16	16	32	
110	89	199		69	111	180	
	F1-N				F2-N		
–	–	–		–	–	–	
15	5	20		20	17	37**	
5	8	13		10	23	33**	
6	16	22	$G=24.489^2$	7	10	17	G=8.638
4	22	26	df=6	5	8	13	df=4*
2	16	18	P<.001	19	8	27	n.s.
6	9	15		28	12	40	
4	9	13		10	10	20	
3	8	11		18	8	26	
45	93	138		49	55	104	
	F1-W				F2-W		
21	21	42		–	–	–	
2	12	14		8	10	18	
4	2	6	$G=21.096^2$	5	1	6	$G=12.072^1$
2	2	4	df=7	2	4	6	df=7
10	5	15	P<.007	3	3	6	n.s.
2	2	4		3	4	7	
1	12	13		14	6	20	
5	5	10		5	14	19	
47	61	108		40	42	82	
				F2 - BY HUTCH SETS			
			F2-E	53	95	148	
			F2-N	69	48	117	$G=14.397^1$
			F2-W	40	42	82	df=2
				162	185	347	P<.001

* C5-N hutches were moved late summer 1990; 1990 nests are included in analyses because most nests were constructed before the hutches were moved. 1991 nests were not included in analyses.

** Hutches were moved in spring, 1987, so 1985 & 1986 were not included in analyses.

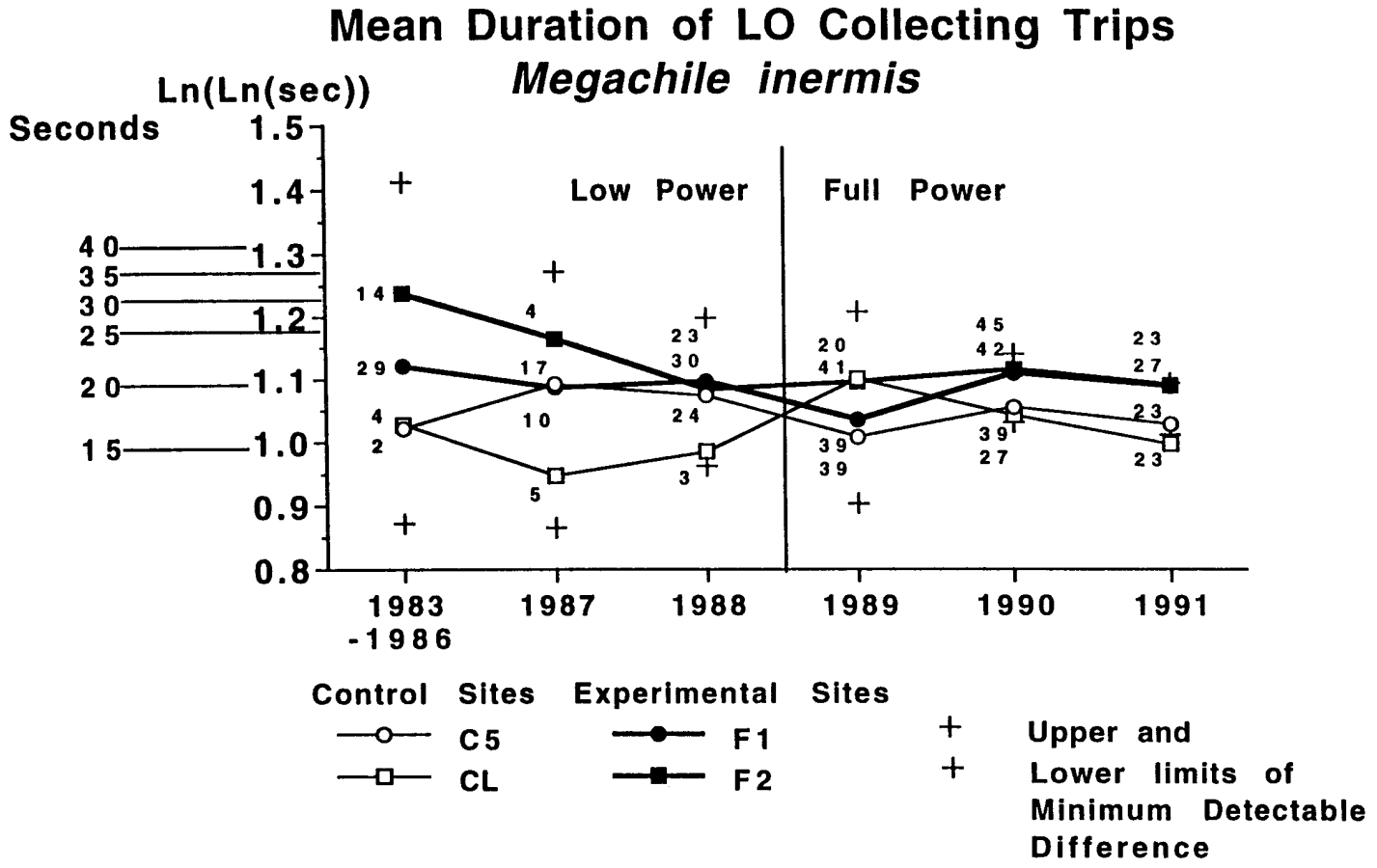


FIGURE 24. Mean duration of LO collecting trips for the first three leaf collecting trips in a cell cap. Numbers indicate number of bees timed; + indicate upper and lower limits to the minimum detectable difference between experimental and control sites for each year.

TABLE 18. GLM of mean of LO trip durations 1987-1991; trips 1-3 for each timed *M. inermis*.

MEAN LO TRIP DURATIONS[1]

Source of variation	Numerator df	MS	F	P>F
Exp	1	0.40	6.19	0.0355*
Site [Exp]	2	0.06	0.72	0.4854
Antenna	1	0.00	0.00	0.9884
Year [Antenna]	3	0.05	0.65	0.5806
Observer [Year * Antenna]	17	0.05	0.65	0.8556
Exp * Antenna	1	0.01	0.09	0.7609
Time [Year * Antenna]	5	0.05	0.62	0.6856
$Time^2$ [Year * Antenna]	5	0.05	0.65	0.6647
Date [Year * Antenna]	5	0.26	3.45	0.0045*
Model	40	0.13	1.71	0.0057*
Error	463	0.08		
$\bar{X}$ = 1.07 (18.4 sec.)	CV = 25.8	R^2 = 0.13		

[1]ln ln transformed

TABLE 18 (continued)

Parameter	Estimate	T for H_0: Parameter = 0	PR> | T |
Exp: Control Sites	-0.053	-1.21	0.2274
Experimental Sites	0.0	–	–
Date [Year * Antenna]			
1987	0.002	0.83	0.4081
1988	0.002	1.17	0.2440
1989	0.002	1.57	0.1165
1990	0.003	3.49	0.0005**
1991	0.001	0.81	0.4167

TABLE 19. *M. relativa* sex ratio by site and year.

	1985			1986		
Site	Males	Females	Ratio	Males	Females	Ratio
C5	98	9	10.9	69	23	3.0
CL	129	49	2.6	75	9	8.3
F1	262	42	6.2	94	18	5.2
F2	129	30	4.3	204	32	6.4
Total	618	130	4.8	442	82	5.4

	1987			1988		
Site	Males	Females	Ratio	Males	Females	Ratio
C5	207	67	3.1	70	25	2.8
CL	55	24	2.3	23	7	3.3
F1	186	60	3.1	111	12	9.3
F2	38	7	5.4	32	9	3.6
Total	486	158	3.1	236	53	4.5

	1989			1990		
Site	Males	Females	Ratio	Males	Females	Ratio
C5	148	70	2.1	125	26	4.8
CL	54	35	1.5	78	16	4.9
F1	95	18	5.3	92	26	3.5
F2	101	21	4.8	221	44	5.0
Total	398	144	2.8	516	112	4.6

	1991			1992		
Site	Males	Females	Ratio	Males	Females	Ratio
C5	61	22	2.8	14	2	7.0
CL	37	12	3.1	44	19	2.3
F1	81	34	2.4	47	32	1.5
F2	186	28	6.6	136	12	11.3
Total	365	96	3.8	241	65	3.7

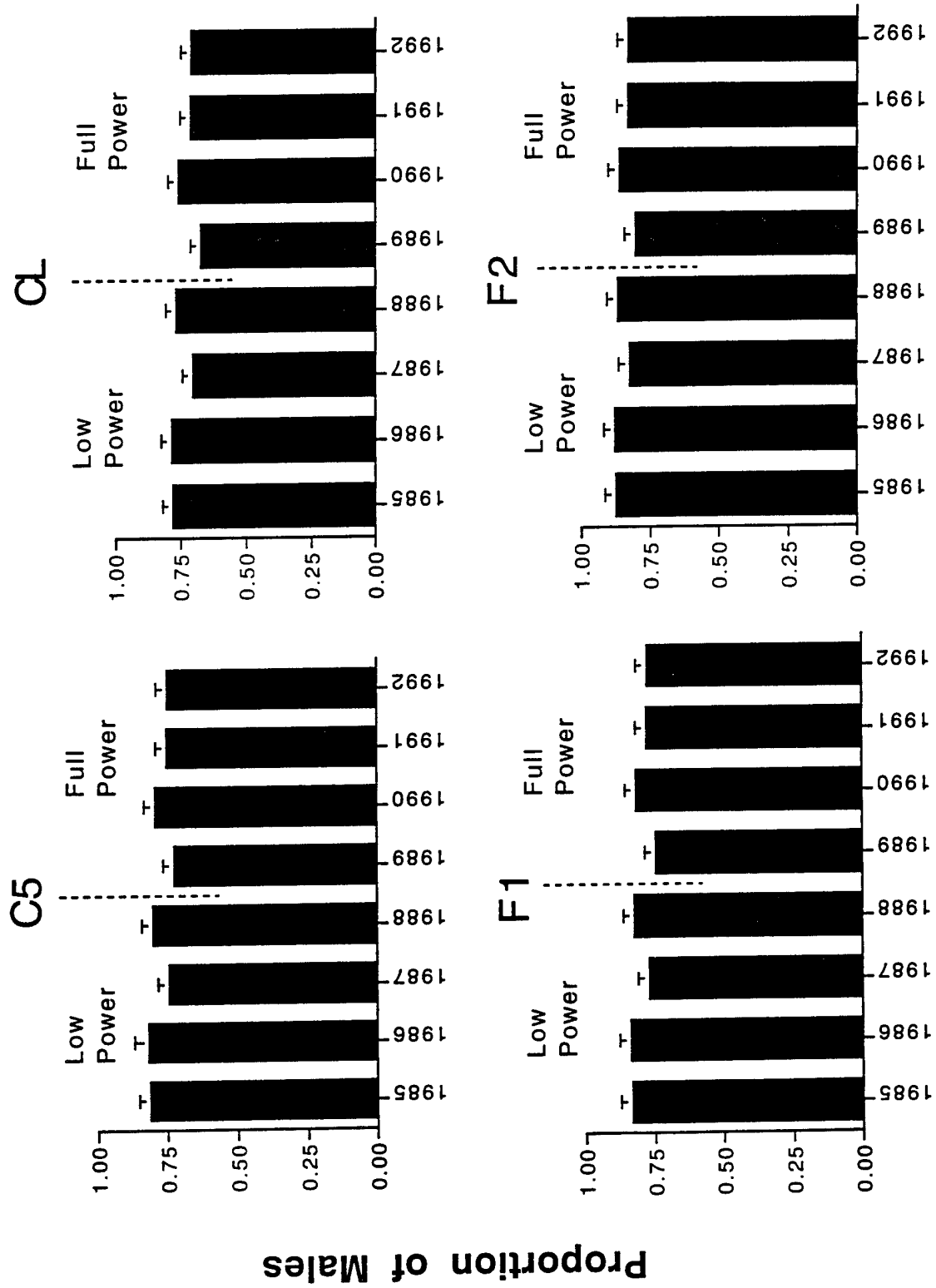


FIGURE 25. Predicted proportion of male *M. relativa* by site and year.

TABLE 20. Categorical modeling analysis of male and female emergences for *M. relativa,* 1985-1992.

SEX RATIO

Source of variation	df	Chi.Square	Prob.
Intercept	1	198.47	0.0000***
Exp	1	26.50	0.0000***
Site [Exp]	2	12.27	0.0022*
Antenna	1	2.15	0.1426
Year [Antenna]	6	20.03	0.0027*
Exp*Antenna	1	0.00	0.9518
Likelihood Ratio	20	87.52	0.0000***

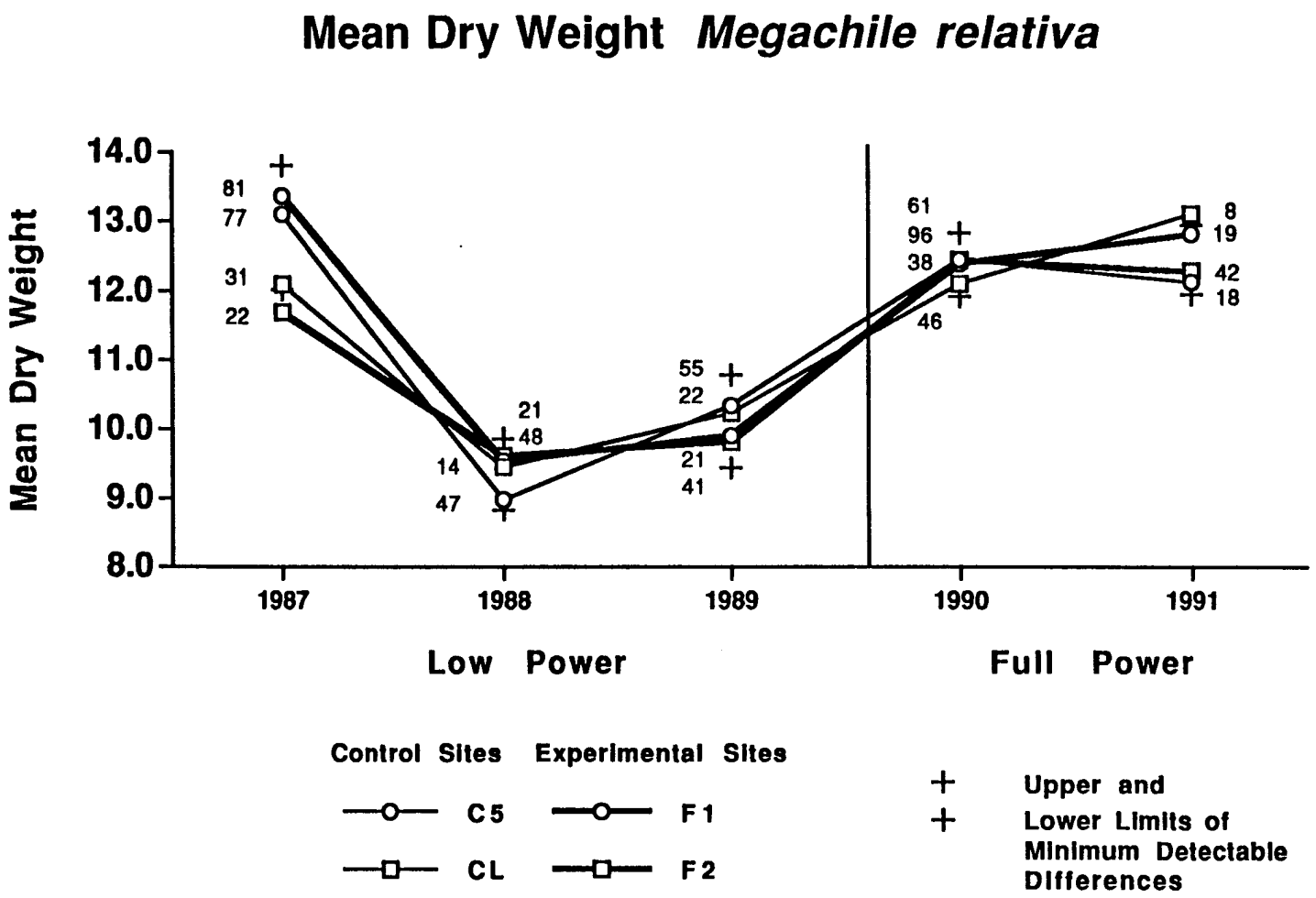


FIGURE 26: Dry weights for *M. relativa* nests, 1987-1991. Numbers indicate sample sizes; + indicates the upper and lower limits to the minimum detectible difference between experimental and control sites for each year.

TABLE 21. GLM of mean dry weights for *M. relativa*, 1987-1991.

DRY WEIGHTS

Source of variation	Numerator df	MS	F	P>F
Exp	1	7.69	1.13	0.3806
Site [Exp]	2	7.60	2.13	0.1197
Antenna	1	12.07	0.04	0.8530
Year [Antenna]	3	424.64	118.89	0.0001***
Exp * Antenna	1	0.26	0.07	0.7888
Sex	1	919.07	257.31	0.0001***
Exp * Sex	1	1.62	0.45	0.5013
Antenna * Sex	1	5.37	1.50	0.2205
Exp * Antenna * Sex	1	0.02	0.01	0.9445
Diameter	1	118.35	33.14	0.0001***
Cells per nest	1	26.68	7.47	0.0064*
Early vs. Late Season	1	62.87	17.60	0.0001***
Sex * Season	1	11.44	3.20	0.0739
Model	16	203.17	56.88	0.0001***
Error	791	3.57		
$\bar{X}$ = 11.6 mg	CV=16.2	R^2=0.54		

TABLE 21 (continued)

Parameter	Estimate:	T for H_0: Parameter = 0	PR>|T|	$\bar{X}$	SE
Year [Antenna]					
1987 Low	3.06	13.7	0.0001***	13.4	0.2
1988 Low	0.0	–	–	10.4	0.2
1989 Full	-2.30	-8.69	0.0001***	10.6	0.2
1990 Full	0.21	0.86	0.3892	13.1	0.1
1991 Full	0.0	–	–	12.9	0.2
Sex: Female	2.41	6.82	0.0001***	13.5	0.2
Male	0.00	–	–	10.7	0.2
Diameter	0.92	5.76	0.0001***		
Cells per nest	0.08	2.73	0.0064*		
Early Season vs.	0.43	2.75	0.0061*	12.4	0.1
Late Season	0.0	–	–	11.7	0.1

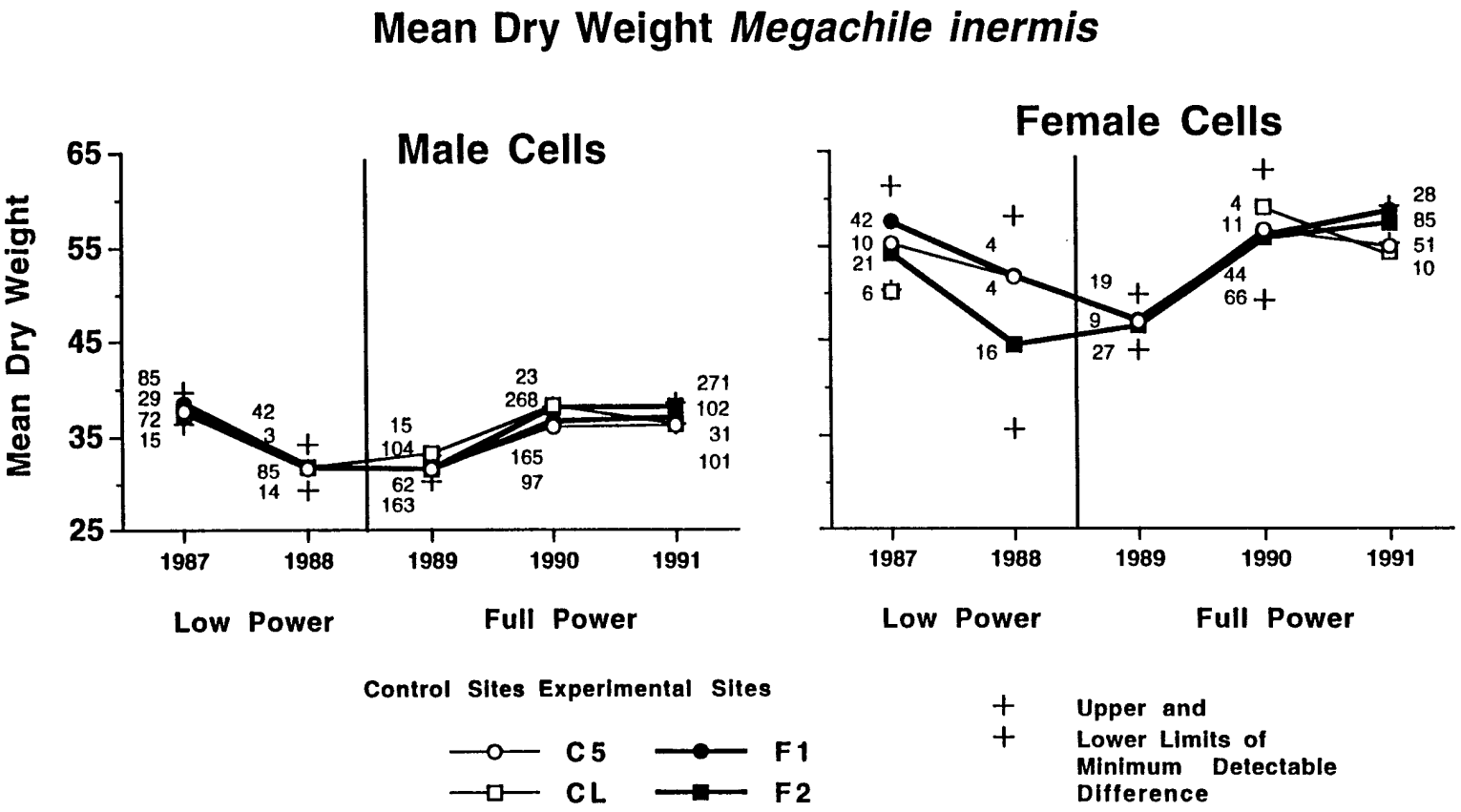


FIGURE 27. Mean dry weight of offspring from *M. inermis* nests by sex 1987-1991, diameters > 9.5mm. Numbers indicate sample sizes; + indicate upper and lower limits to the minimum detectable difference between experimental and control sites for each year.

TABLE 22. GLM of mean dry weights for *M. inermis*; diameters > 9.5mm; 1987-1991.

DRY WEIGHTS

Source of variation	Numerator df	MS	F	P>F
Exp	1	162.96	4.63	0.0336*
Site [Exp]	2	16.41	0.39	0.6801
Antenna	1	24.95	0.25	0.8834
Year [Antenna]	3	3304.30	77.610	0.0001***
Exp. * Antenna	1	11.02	0.259	0.6110
Sex	1	41119.23	965.79	0.0001***
Exp. * Sex	1	0.29	0.01	0.9342
Antenna * Sex	1	74.01	1.74	0.1875
Exp * Antenna * Sex	1	0.93	0.02	0.8823
Diameter	1	1113.61	26.16	0.0001***
Cells per nest	1	395.28	9.28	0.0023*
Early vs. Late Season	1	1401.61	32.92	0.0001***
Sex * Season	1	325.35	7.64	0.0058*
Model	16	157871.25	231.75	0.0***
Error	2187	42.58		
$\bar{X}$ = 39.8mg	CV = 16.4	R^2 = 0.63		

TABLE 22 (continued)

Parameter	Estimate	T for H_0: Parameter = 0	PR > |T|	$\bar{X}$	SE
Exp:					
Control	-1.32	-2.88	0.0040*	43.1	0.5
Treatment	0.0	–	–	44.2	0.3
Year [Antenna]:					
1987 Low	6.37	9.56	0.0001***	46.7	0.5
1988 Low	0.0	–	–	40.3	0.7
1989 Full	-5.73	-11.14	0.0001***	40.1	0.5
1990 Full	-0.16	-0.42	0.6725	45.7	0.4
1991 Full	0.0	–	–	45.9	0.4
Sex F	19.22	26.38	0.0001***	52.4	0.5
M	0.0	–	–	35.0	0.3
Diameter	1.72	5.11	0.0001***		
Cells per Nest	0.38	3.05	0.0023*		
Season:					
Early vs	3.48	9.77	0.0001***	44.9	0.3
Late	0.0	–	–	42.5	0.4
Sex * Season					
F Early	-2.19	-2.76	0.0058*	53.1	0.5
F Late	0.0	–	–	51.8	0.7
M Early	0.0	–	–	36.7	0.3
M Late	0.0	–	–	33.2	0.4

TABLE 23. Late summer emergences (% bivoltinism) of *M. relativa* and *Coelioxys* spp.

M. relativa

Year	cells emerging late summer / total cells emerging[1]	(%)	nests emerging late summer / total nests emerging[1]	(%)
1987	33/629	(5.2%)	7/186	(3.8%)
1988	13/285	(4.6%)	7/144	(4.9%)
1989	112/515	(21.7%)	24/166	(14.5%)
1990	41/621	(6.6%)	13/232	(5.6%)
1991	26/452	(5.8%)	7/165	(4.2%)
1992	25/282	(8.9%)	9/126	(7.1%)

Coelioxys spp.

Year	cells emerging late summer / total cells emerging[2]	(%)	nests emerging late summer / total nests emerging[2]	(%)
1987	11/99	(11.1%)	10/77	(13.0%)
1988	10/87	(11.5%)	8/62	(12.9%)
1989	18/71	(25.4%)	11/50	(22.0%)
1990	7/116	(6.0%)	6/92	(6.5%)
1991	12/107	(11.2%)	12/75	(16.0%)
1992	1/79	(1.3%)	1/61	(1.6%)

[1]Total cells or nests with adult *M. relativa*.

[2]Total cells or nests with adult *Coelioxys* in *M. relativa* nests.

TABLE 24. Late summer emergences (% bivoltinism) of *M. inermis* and *Coelioxys* spp.

M. inermis

Year	cells emerging late summer / total cells emerging[1]	(%)	nests emerging late summer / total nests emerging[1]	(%)
1987	2/1011	(0.2%)	1/262	(0.4%)
1988	0/562	(0.0%)	0/168	(0.0%)
1989	4/1190	(0.3%)	1/400	(0.3%)
1990	5/1969	(0.3%)	1/628	(0.2%)
1991	4/2160	(0.2%)	1/606	(0.2%)
1992	0/1186	(0.0%)	0/317	(0.0%)

Coelioxys spp.

Year	cells emerging late summer / total cells emerging[2]	(%)	nests emerging late summer / total nests emerging[2]	(%)
1987	0/62	(0.0%)	0/48	(0.0%)
1988	0/18	(0.0%)	0/16	(0.0%)
1989	0/86	(0.0%)	0/67	(0.0%)
1990	0/85	(0.0%)	0/70	(0.0%)
1991	0/51	(0.0%)	0/48	(0.0%)
1992	0/124	(0.0%)	0/102	(0.0%)

[1]Total cells or nests with adult *M. inermis*.

[2]Total cells or nests with adult *Coelioxys* in *M. inermis* nests.

TABLE 25. Proportion of *M. relativa* mortality from various sources by site.

Stage or source of mortality	SITE C5	CL	F1	F2
1985				
Pre-overwintering (egg & larvae)	0.185	0.131	0.059	0.053
Overwintering (Prepupae)	0.045	0.069	0.014	0.041
Total parasitism	0.089	0.073	0.100	0.254
(*Coelioxys* only)	(0.076)	(0.053)	(0.089)	(0.234)
Post-overwintering Survival*	0.681	0.727	0.827	0.652
1986				
Pre-overwintering (egg & larvae)	0.104	0.138	0.109	0.041
Overwintering (Prepupae)	0.130	0.015	0.085	0.063
Total parasitism	0.169	0.177	0.127	0.149
(*Coelioxys* only)	(0.130)	(0.138)	(0.127)	(0.114)
Post-overwintering Survival*	0.597	0.669	0.679	0.749
1987				
Pre-overwintering (egg & larvae)	0.235	0.354	0.186	0.344
Overwintering (Prepupae)	0.041	0.030	0.055	0.070
Total parasitism	0.058	0.128	0.118	0.234
(*Coelioxys* only)	(0.041)	(0.122)	(0.110)	(0.195)
Post-overwintering Survival*	0.665	0.488	0.640	0.352
1988				
Pre-overwintering (egg & larvae)	0.313	0.407	0.363	0.464
Overwintering (Prepupae)	0.134	0.122	0.106	0.064
Total parasitism	0.167	0.228	0.099	0.144
(*Coelioxys* only)	(0.138)	(0.195)	(0.070)	(0.128)
Post-overwintering Survival*	0.386	0.244	0.433	0.328

* Includes cells with dead pupae, dead adults, and successfully emerging adult *M. relativa*.

TABLE 25 (continued)

Stage or source of mortality	SITE C5	CL	F1	F2
1989				
Pre-overwintering (egg & larvae)	0.106	0.127	0.080	0.176
Overwintering (Prepupae)	0.165	0.127	0.105	0.188
Total parasitism	0.083	0.206	0.117	0.130
(*Coelioxys* only)	(0.071)	(0.139)	(0.111)	(0.092)
Post-overwintering Survival*	0.646	0.539	0.698	0.506
1990				
Pre-overwintering (egg & larvae)	0.095	0.201	0.179	0.116
Overwintering (Prepupae)	0.069	0.082	0.067	0.067
Total parasitism	0.182	0.207	0.101	0.136
(*Coelioxys* only)	(0.147)	(0.179)	(0.101)	(0.105)
Post-overwintering Survival*	0.654	0.511	0.654	0.681
1991				
Pre-overwintering (egg & larvae)	0.223	0.291	0.136	0.090
Overwintering (Prepupae)	0.072	0.127	0.043	0.093
Total parasitism	0.205	0.216	0.111	0.182
(*Coelioxys* only)	(0.193)	(0.142)	(0.105)	(0.146)
Post-overwintering Survival*	0.500	0.366	0.710	0.636
1992				
Pre-overwintering (egg & larvae)	0.323	0.376	0.252	0.170
Overwintering (Prepupae)	0.123	0.045	0.105	0.069
Total parasitism	0.308	0.105	0.091	0.225
(*Coelioxys* only)	(0.308)	(0.098)	(0.063)	(0.203)
Post-overwintering Survival*	0.246	0.474	0.552	0.536

* Includes cells with dead pupae, dead adults, and successfully emerging adult *M. relativa*.

TABLE 26. Proportion of *M. inermis* mortality from various sources by site.

Stage or source of mortality	SITE C5	CL	F1	F2
1985				
Pre-overwintering (egg & larvae)	0.151	0.098	0.184	0.114
Overwintering (Prepupae)	0.019	0.000	0.028	0.022
Total parasitism	0.189	0.176	0.031	0.079
(*Coelioxys* only)	(0.170)	(0.059)	(0.011)	(0.035)
Post-overwintering Survival*	0.641	0.725	0.757	0.786
1986				
Pre-overwintering (egg & larvae)	0.119	0.000	0.061	0.004
Overwintering (Prepupae)	0.051	0.000	0.038	0.026
Total parasitism	0.068	0.000	0.167	0.073
(*Coelioxys* only)	(0.034)	(0.000)	(0.038)	(0.009)
Post-overwintering Survival*	0.763	1.000	0.735	0.897
1987				
Pre-overwintering (egg & larvae)	0.272	0.062	0.131	0.124
Overwintering (Prepupae)	0.092	0.062	0.055	0.069
Total parasitism	0.072	0.186	0.070	0.103
(*Coelioxys* only)	(0.048)	(0.088)	(0.032)	(0.041)
Post-overwintering Survival*	0.564	0.690	0.744	0.704
1988				
Pre-overwintering (egg & larvae)	0.174	0.300	0.175	0.260
Overwintering (Prepupae)	0.165	0.100	0.087	0.085
Total parasitism	0.035	0.150	0.044	0.060
(*Coelioxys* only)	(0.009)	(0.150)	(0.000)	(0.025)
Post-overwintering Survival*	0.626	0.450	0.694	0.595

* Includes cells with dead pupae, dead adults, and successfully emerging adult *M. inermis*.

TABLE 26 (continued)

Stage or source of mortality	SITE C5	CL	F1	F2 overwintered C5	F2
1989					
Pre-overwintering (egg & larvae)	0.183	0.156	0.130		0.171
Overwintering (Prepupae)	0.214	0.167	0.213		0.240
Total parasitism	0.060	0.156	0.099		0.062
(*Coelioxys* only)	(0.036)	(0.115)	(0.042)		(0.032)
Post-overwintering Survival*	0.542	0.521	0.558		0.527
1990					
Pre-overwintering (egg & larvae)	0.206	0.249	0.137	0.074	0.069
Overwintering (Prepupae)	0.159	0.180	0.186	0.164	0.214
Total parasitism	0.091	0.152	0.078	0.057	0.083
(*Coelioxys* only)	(0.042)	(0.106)	(0.013)	(0.021)	(0.028)
Post-overwintering Survival*	0.543	0.419	0.599	0.706	0.634
1991					
Pre-overwintering (egg & larvae)	0.151	0.258	0.200	0.105	0.144
Overwintering (Prepupae)	0.072	0.146	0.079	0.074	0.089
Total parasitism	0.057	0.100	0.090	0.059	0.074
(*Coelioxys* only)	(0.007)	(0.029)	(0.017)	(0.014)	(0.023)
Post-overwintering Survival*	0.719	0.496	0.630	0.761	0.693
1992					
Pre-overwintering (egg & larvae)	0.128	0.120	0.150		0.120
Overwintering (Prepupae)	0.057	0.032	0.048		0.034
Total parasitism	0.088	0.057	0.101		0.128
(*Coelioxys* only)	(0.048)	(0.038)	(0.072)		(0.102)
Post-overwintering Survival*	0.727	0.791	0.701		0.718

* Includes cells with dead pupae, dead adults, and successfully emerging adult *M. inermis*.

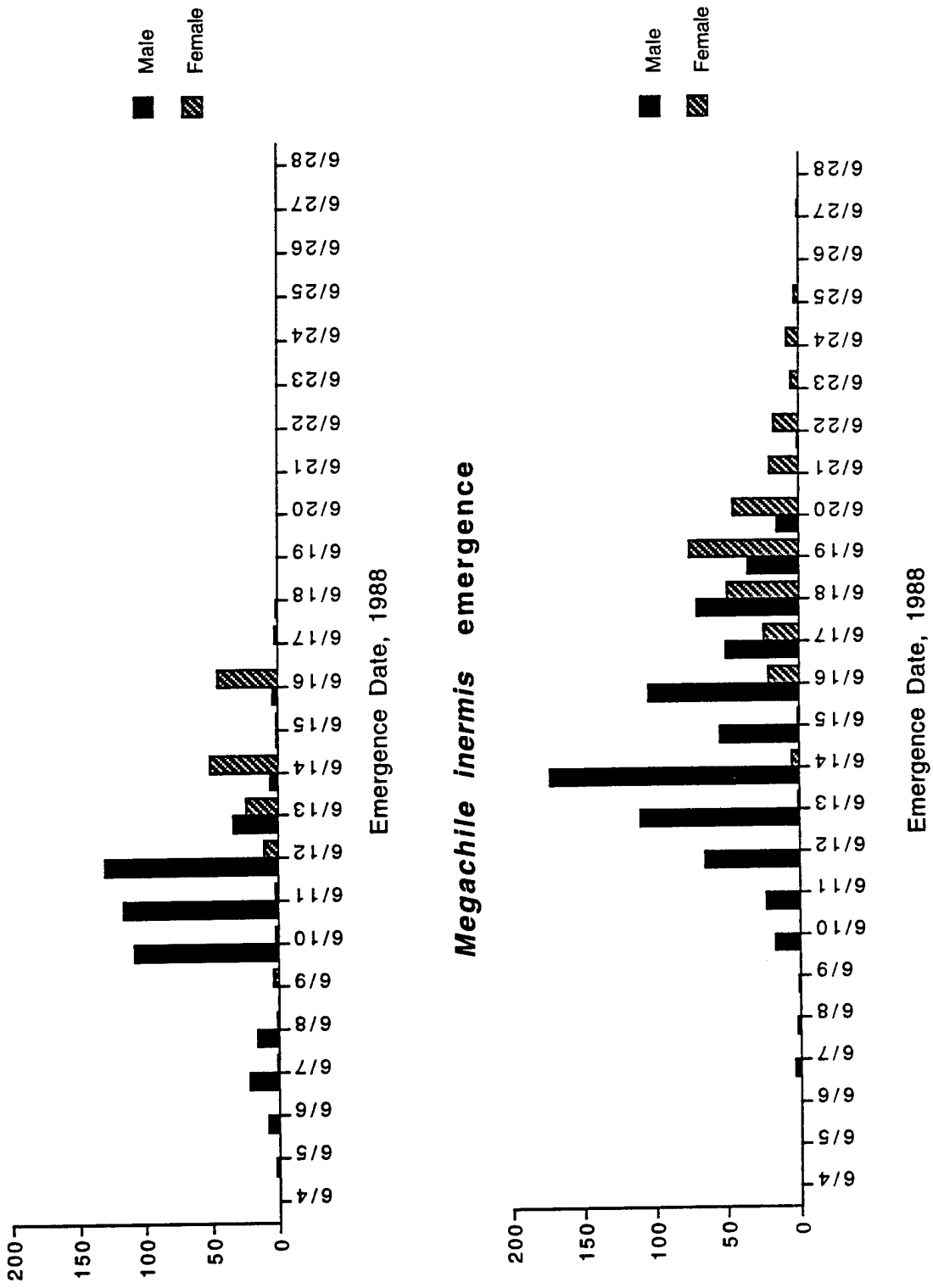


FIGURE 28. Phenology of emergence, 1987 nests emerging in 1988.

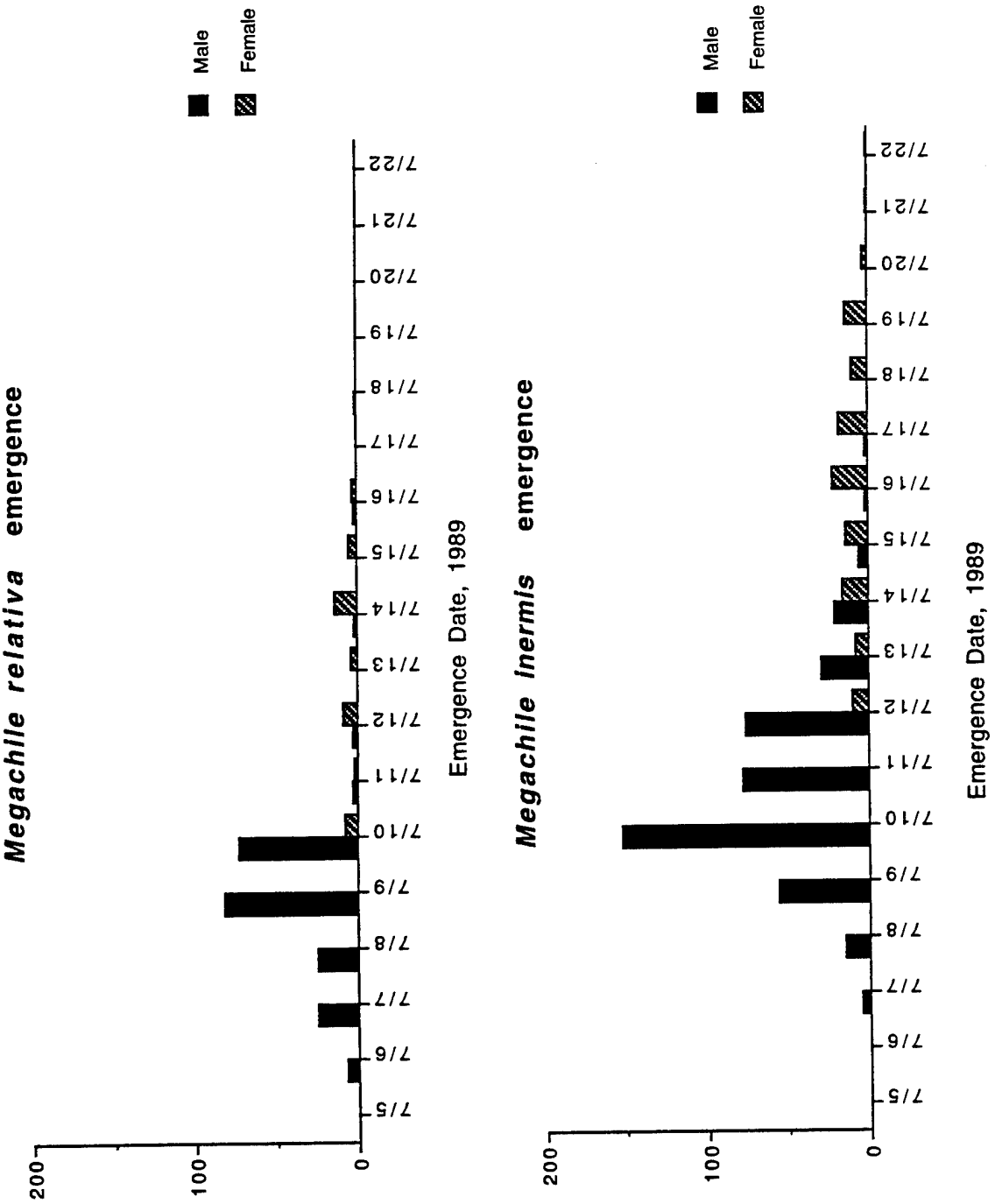


FIGURE 29. Phenology of emergence, 1988 nests emerging in 1989.

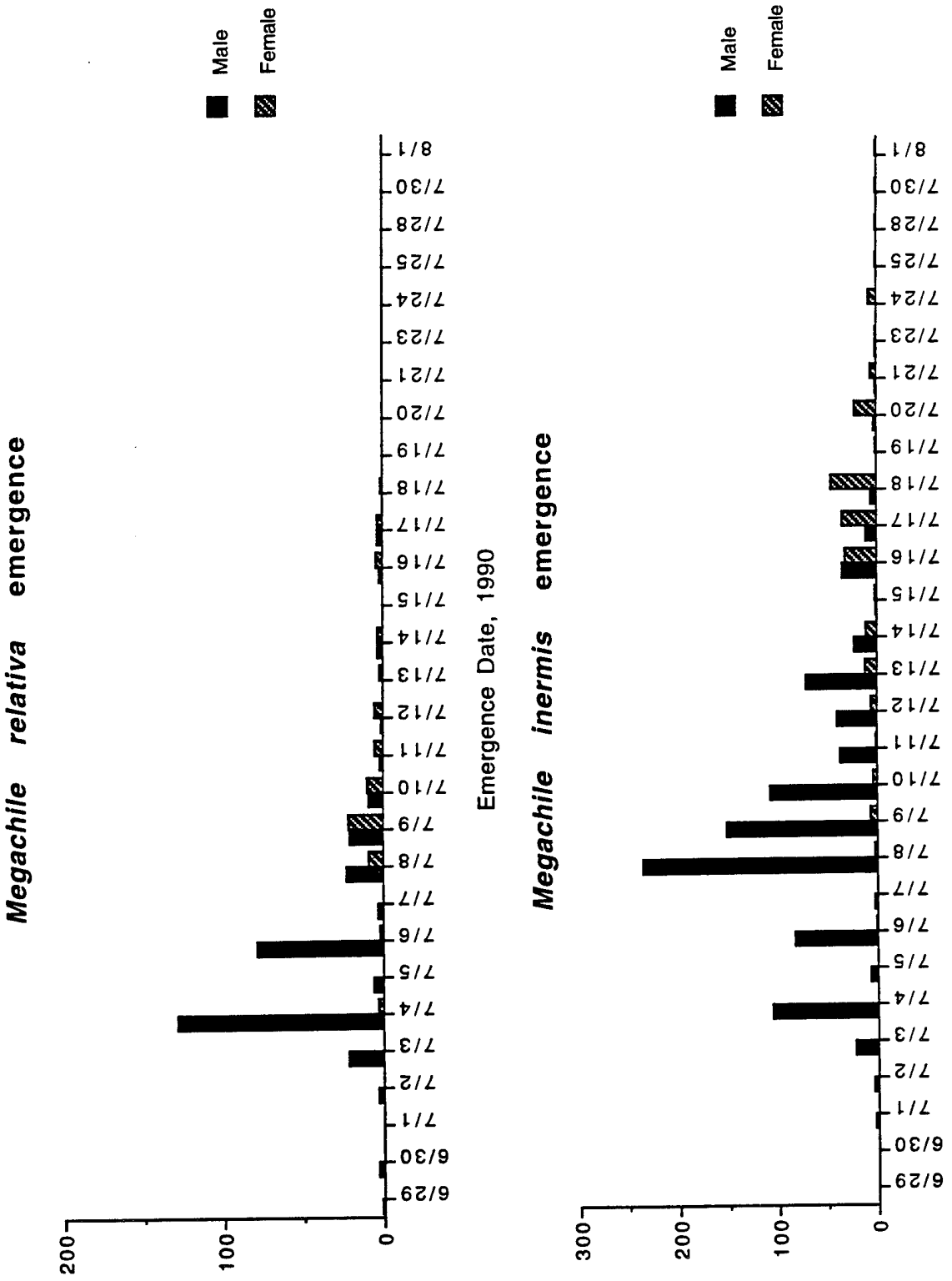


FIGURE 30. Phenology of emergence, 1989 nests emerging in 1990.

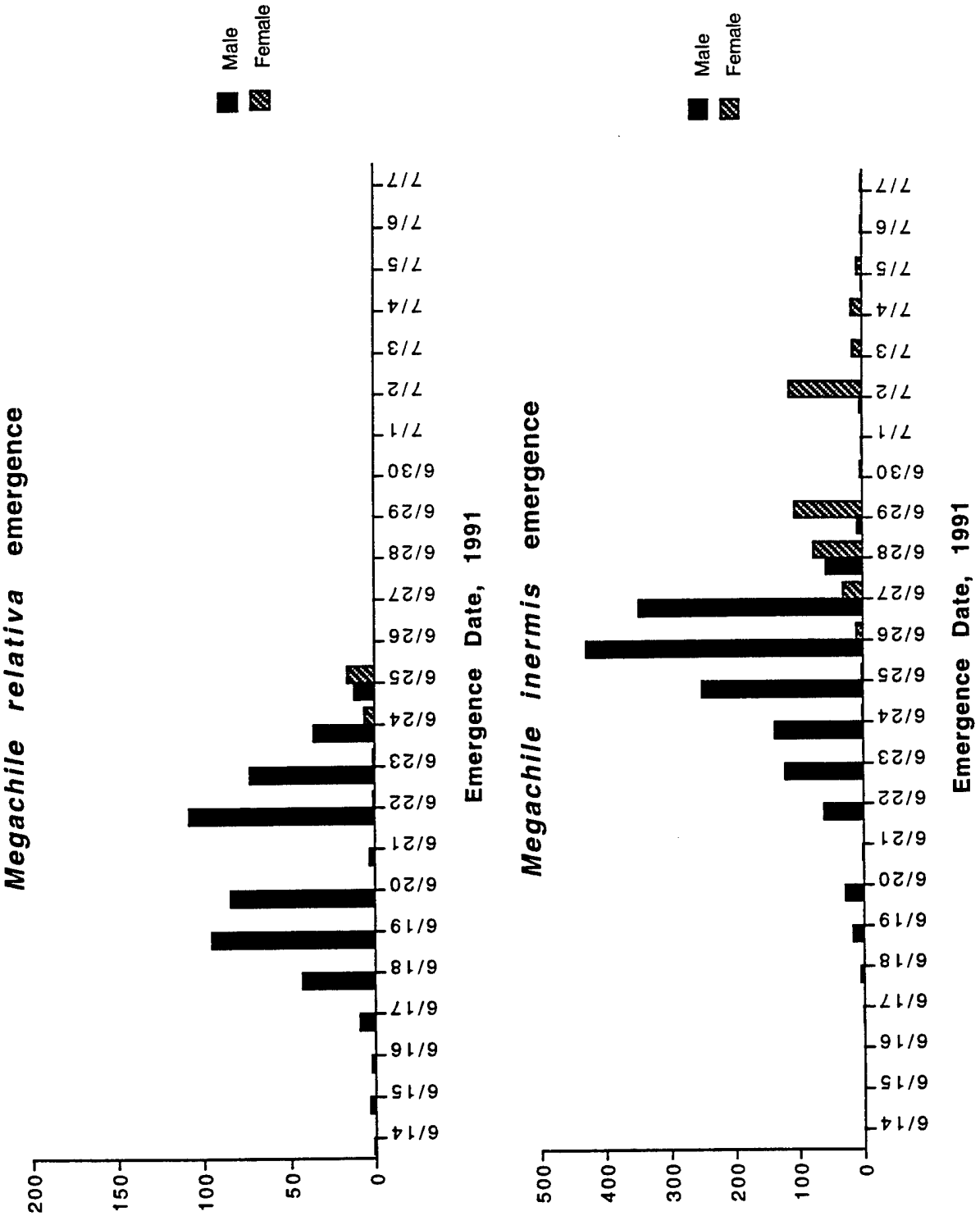


FIGURE 31. Phenology of emergence, 1990 nests emerging in 1991.

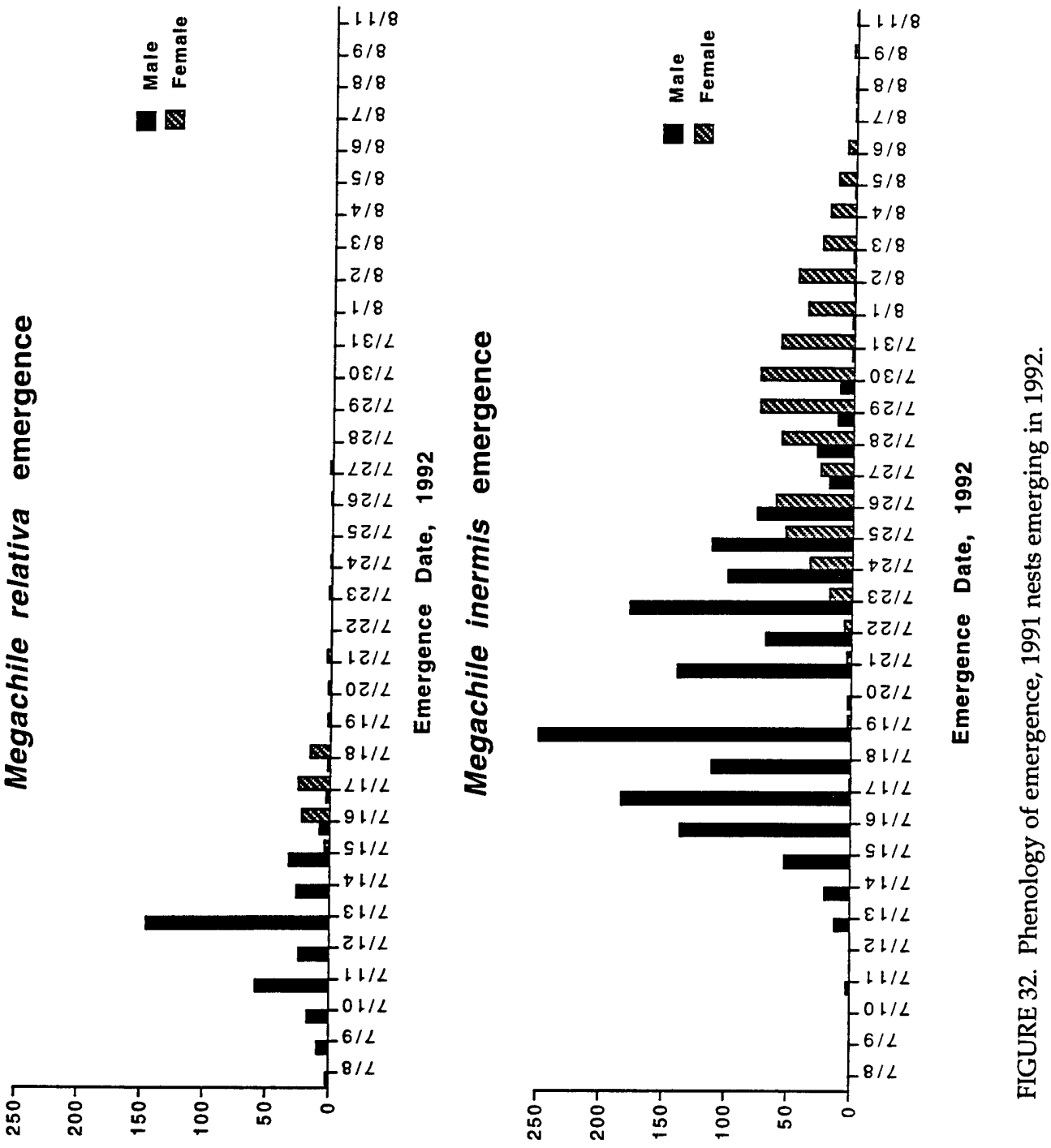
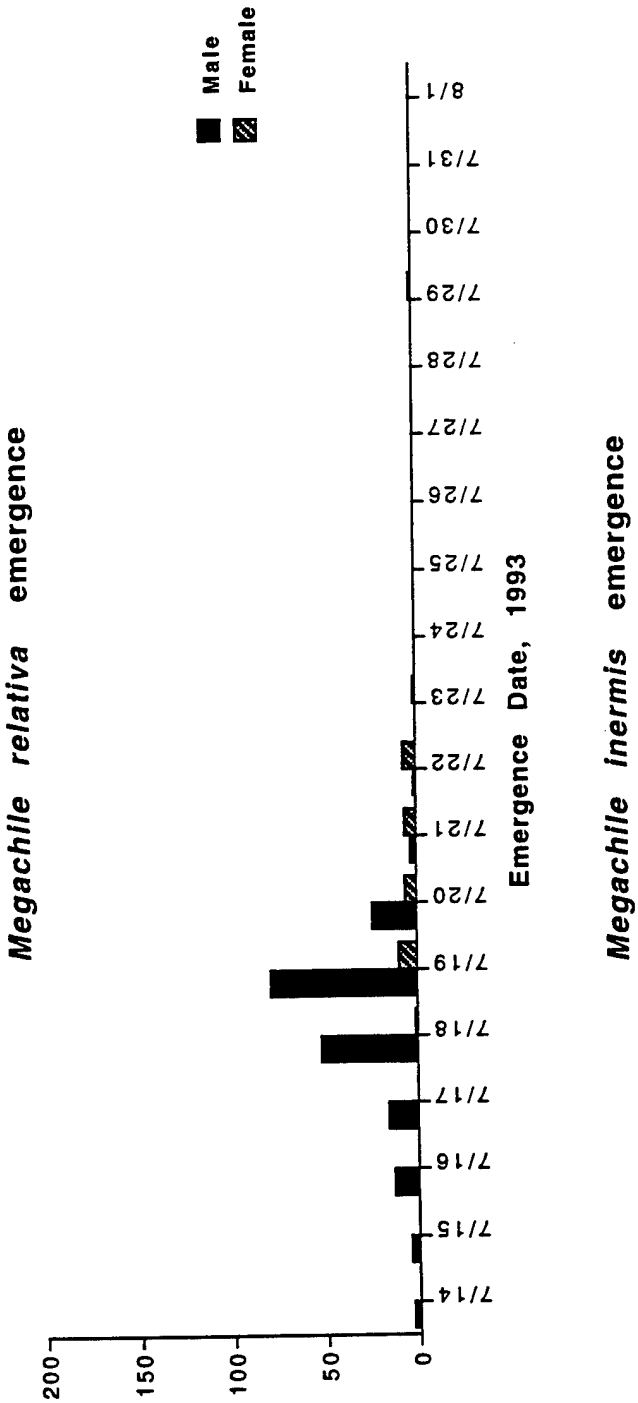


FIGURE 32. Phenology of emergence, 1991 nests emerging in 1992.



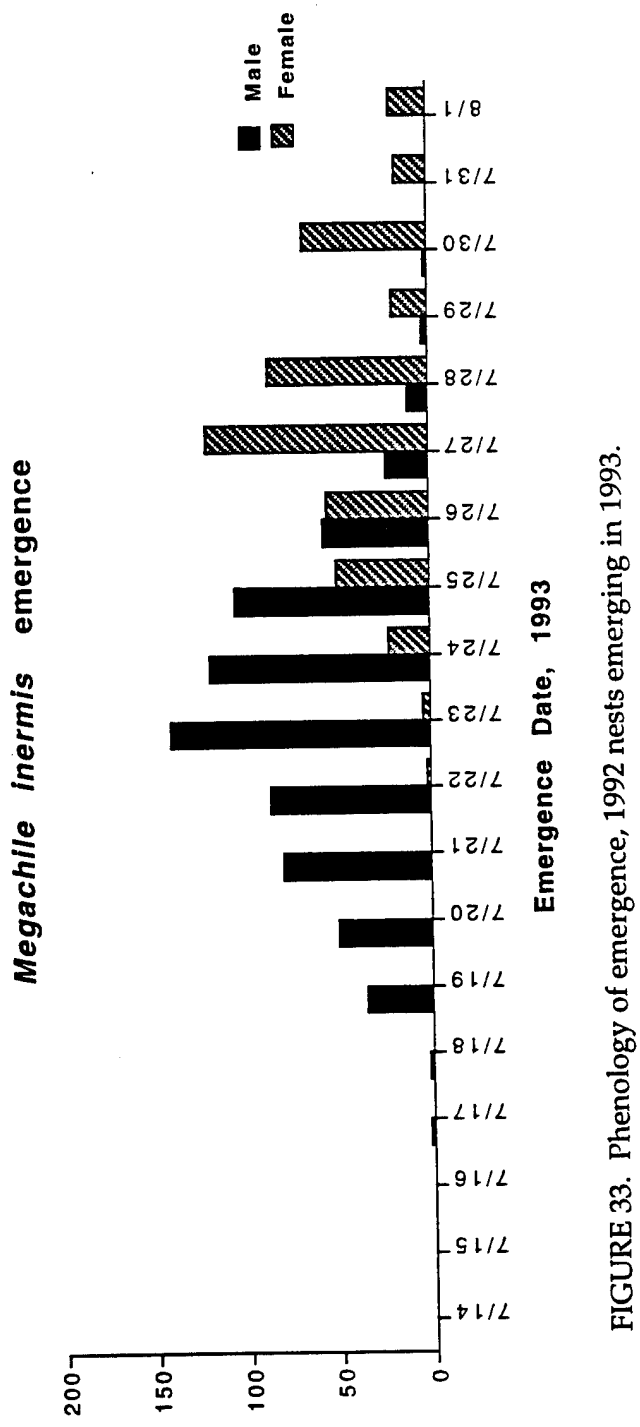


FIGURE 33. Phenology of emergence, 1992 nests emerging in 1993.

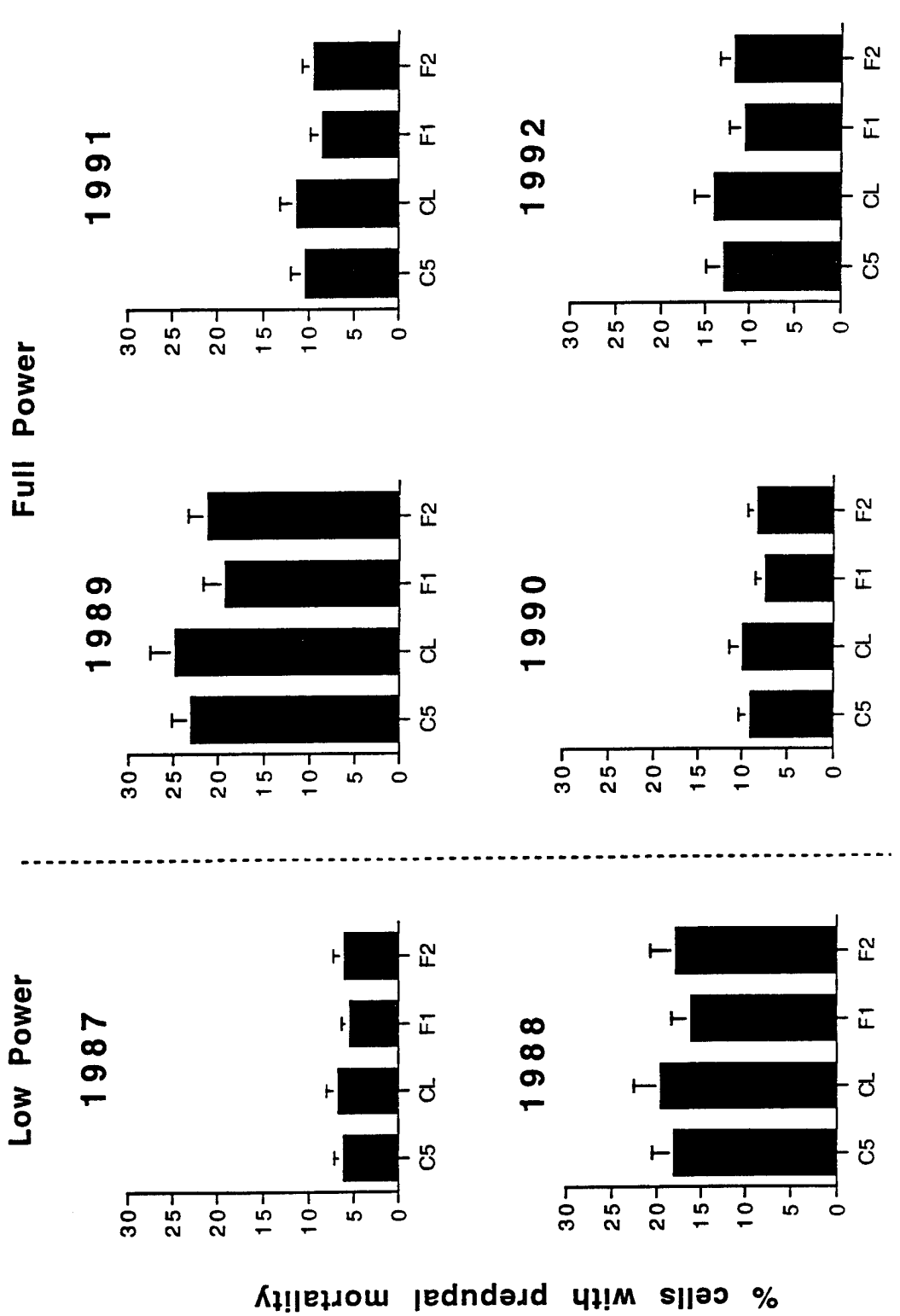


FIGURE 34a. Predicted percent of cells with prepupal mortality by year and site, *M. relativa*.

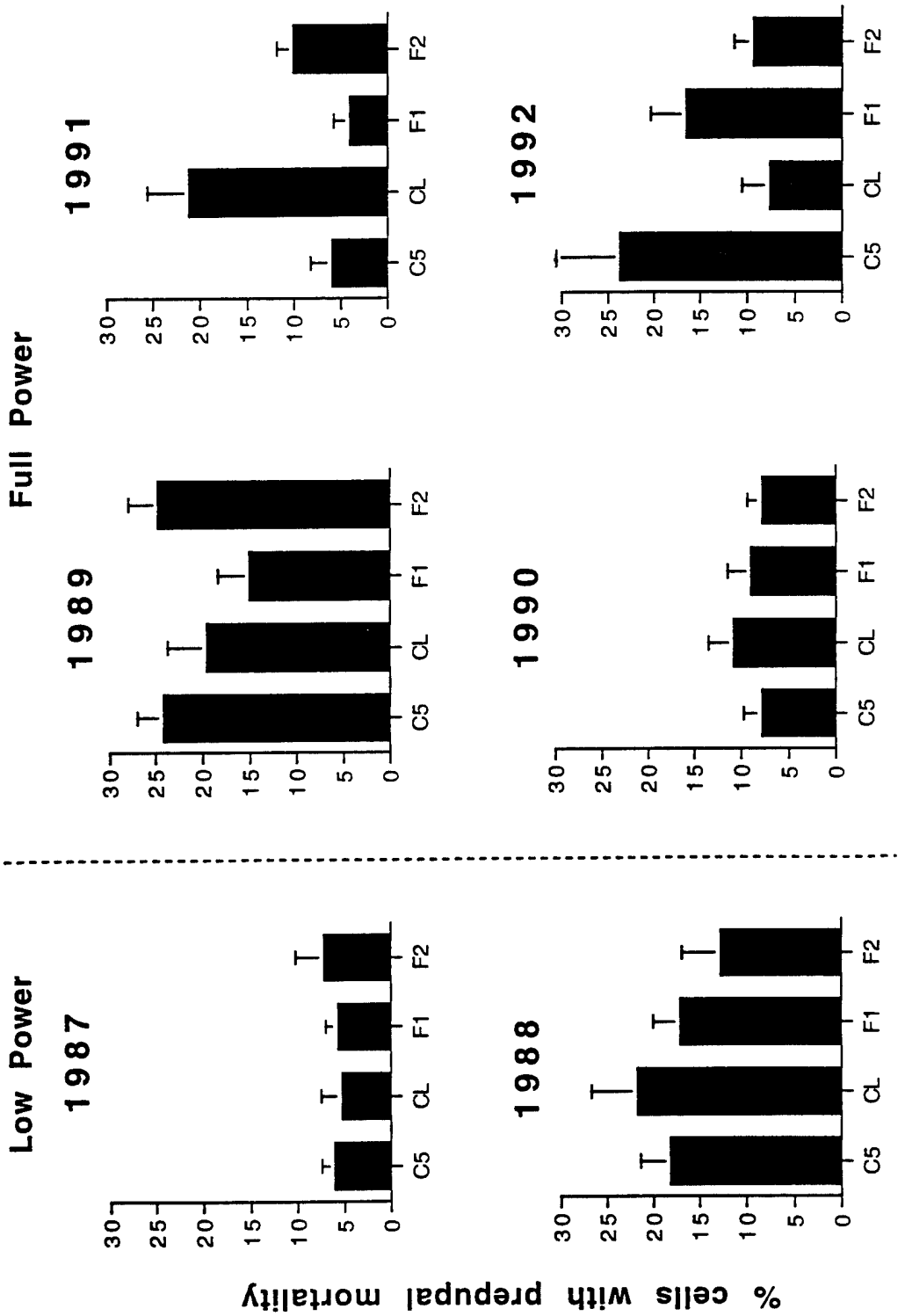


FIGURE 34b. Actual percent of cells with prepupal mortality by year and site, *M. relativa*.

TABLE 27. Categorical modeling analysis of cells with prepupal mortality vs. cells with pupae and adults for *M. relativa*, 1987 - 1992.

PROPORTION OF CELLS WITH PREPUPAL MORTALITY

Source of variation	df	Chi-Square	Prob.
Intercept	1	362.15	0.0000***
Exp	1	2.51	0.1135
Site [Exp]	2	0.76	0.6854
Antenna	1	8.53	0.0035*
Year [Antenna]	4	90.62	0.0000***
Exp * Antenna	1	0.19	0.6627
Residual	14	30.24	0.0071*

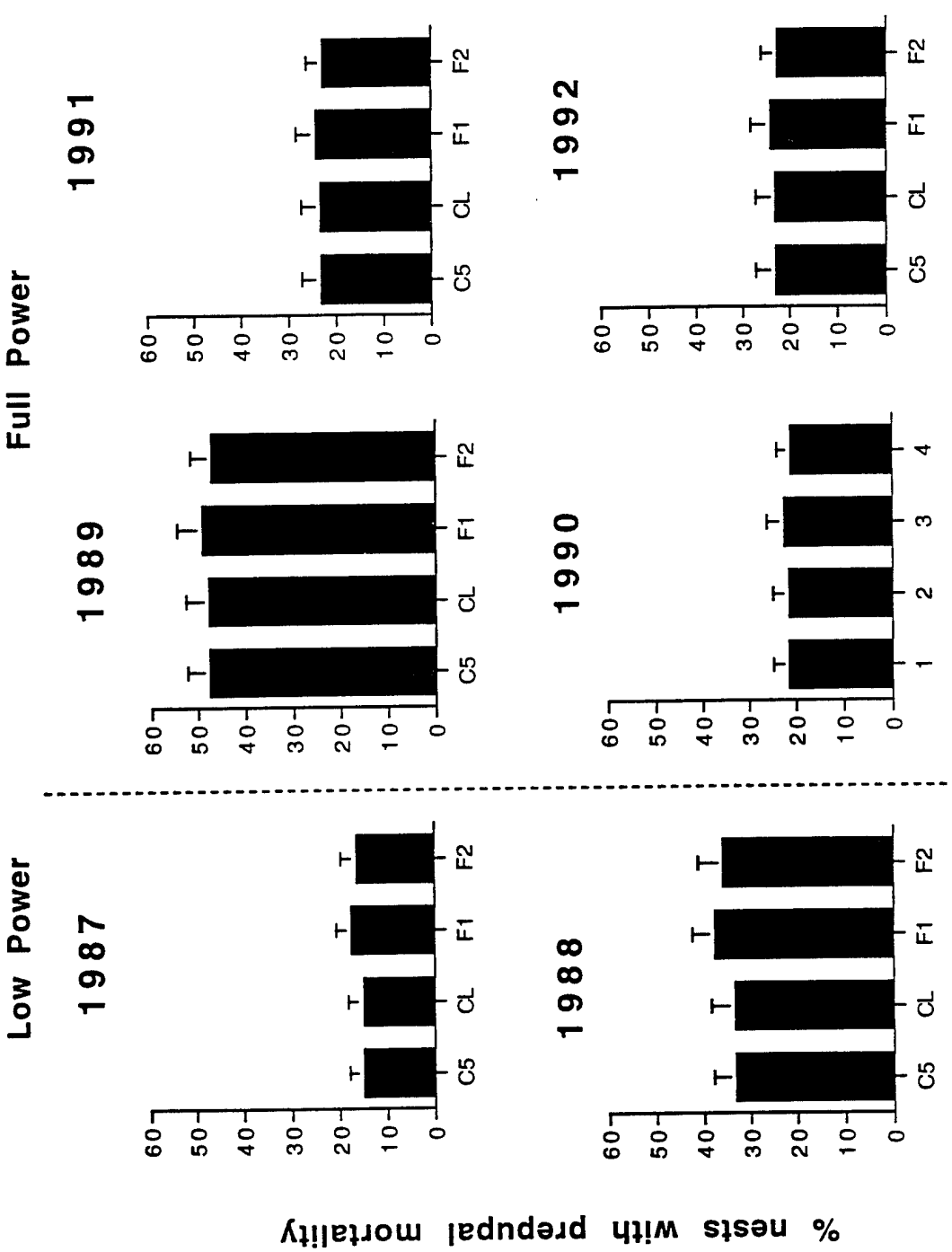


FIGURE 35a. Predicted percent of nests with prepupal mortality by year and site, *M. relativa*.

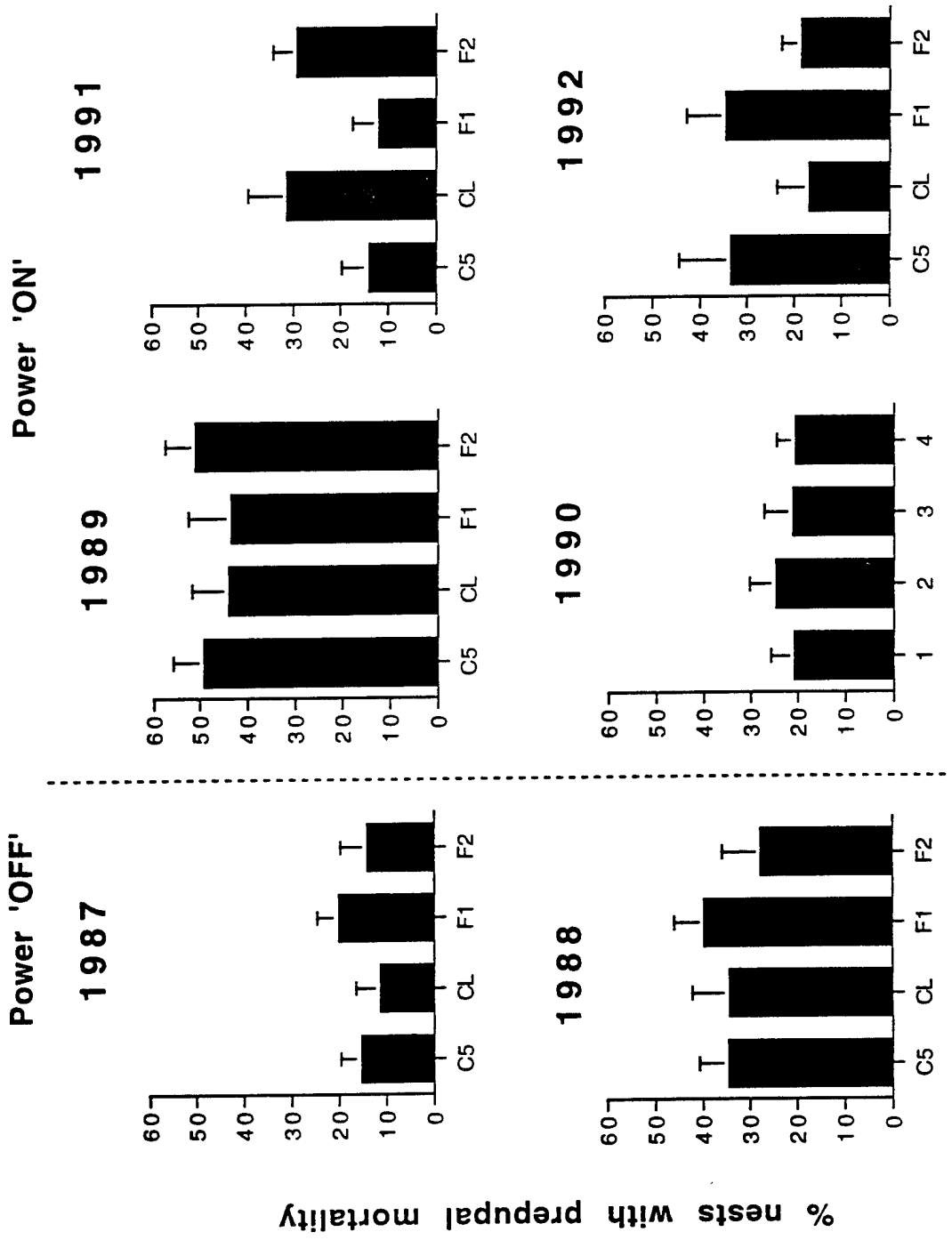


Figure 35b. Actual percent of nests with prepupal mortality by year and site, *M. relativa*.

TABLE 28. Categorical modeling analysis of nests with prepupal mortality vs. nests with pupae and adults for *M. relativa*, 1987 - 1992.

PROPORTION OF NESTS WITH PREPUPAL MORTALITY

Source of variation	df	Chi-Square	Prob.
Intercept.	1	51.74	0.0000***
Exp	1	0.31	0.5765
Site [Exp]	2	0.33	0.8461
Antenna	1	3.78	0.0518
Year [Antenna]	4	57.39	0.0000***
Exp * Antenna	1	0.17	0.6817
Residual	14	14.84	0.3893

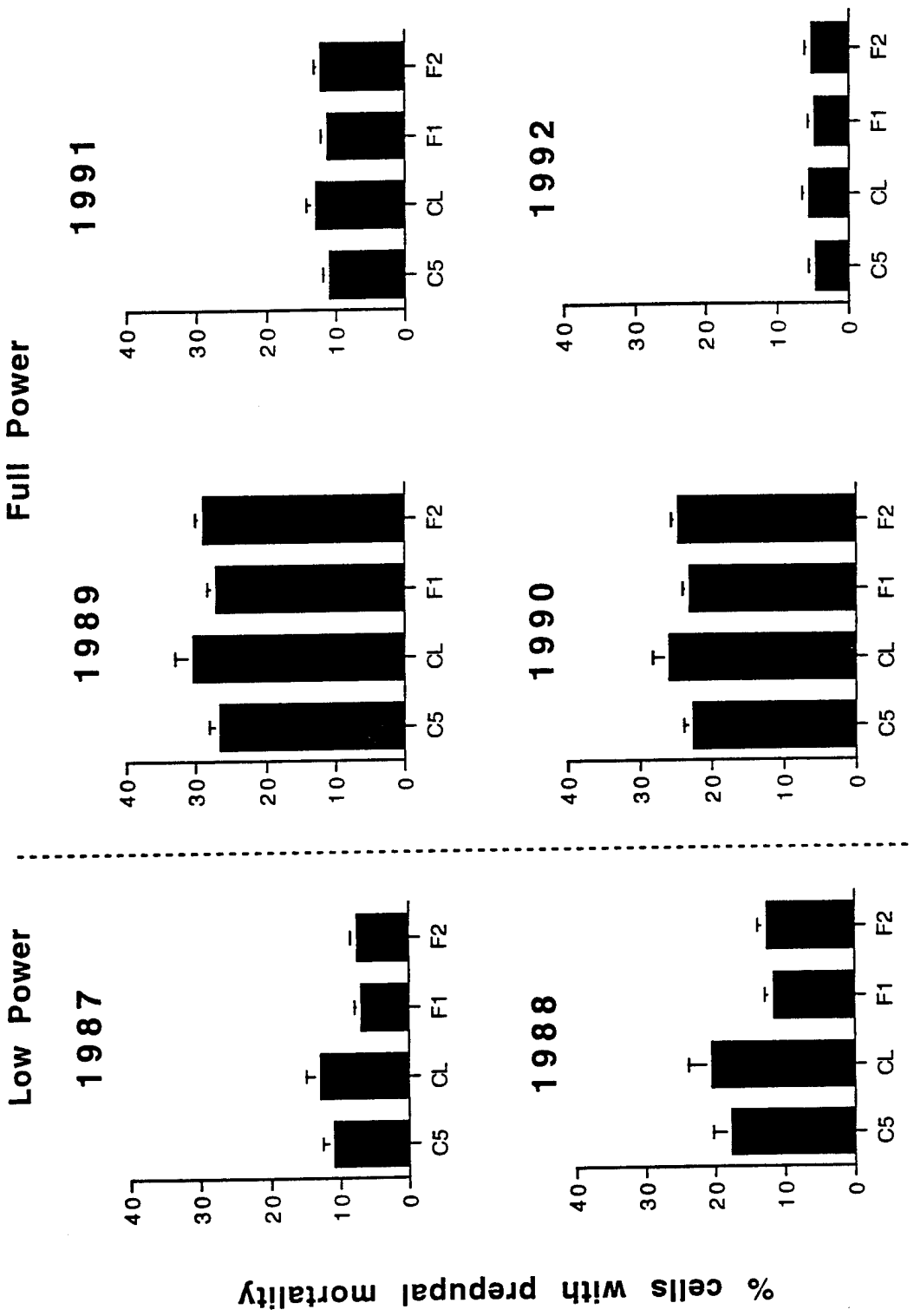


FIGURE 36a. Predicted percent of cells with prepupal mortality by year and site, *M. inermis*.

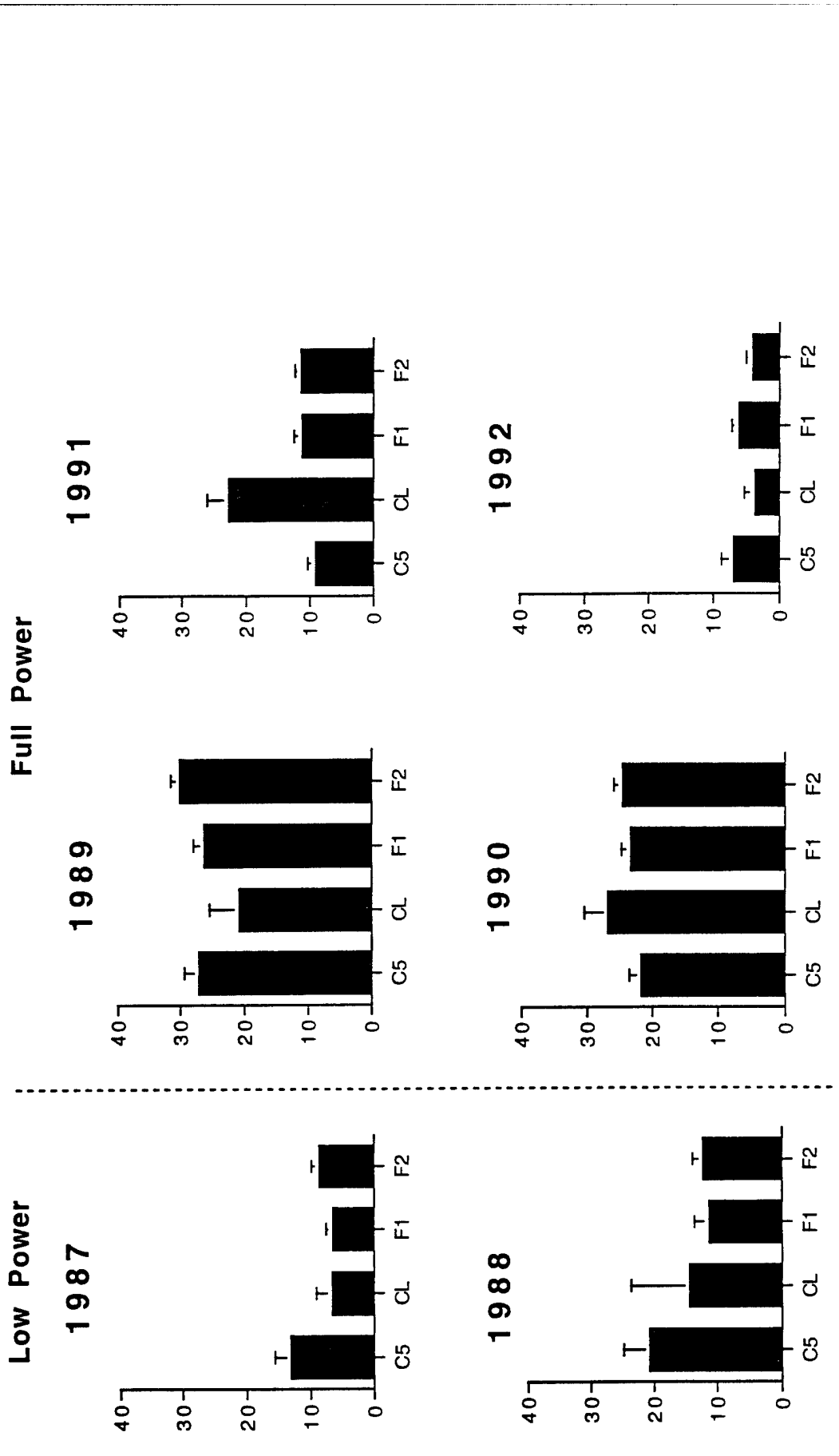


Figure 36b. Actual percent of cells with prepupal mortality by year and site, *M. inermis*.

TABLE 29. Categorical modeling analysis of cells with prepupal mortality vs. cells with pupae and adults for *M. inermis*, 1987 - 1992.

PROPORTION OF CELLS WITH PREPUPAL MORTALITY

Source of variation	df	Chi-Square	Prob.
Intercept	1	627.67	0.0000***
Exp	1	10.83	0.0010**
Site [Exp]	2	5.98	0.0504
Antenna	1	4.35	0.0371*
Year [Antenna]	4	351.91	0.0000***
Exp * Antenna	1	8.46	0.0036*
Residual	14	30.96	0.0056*

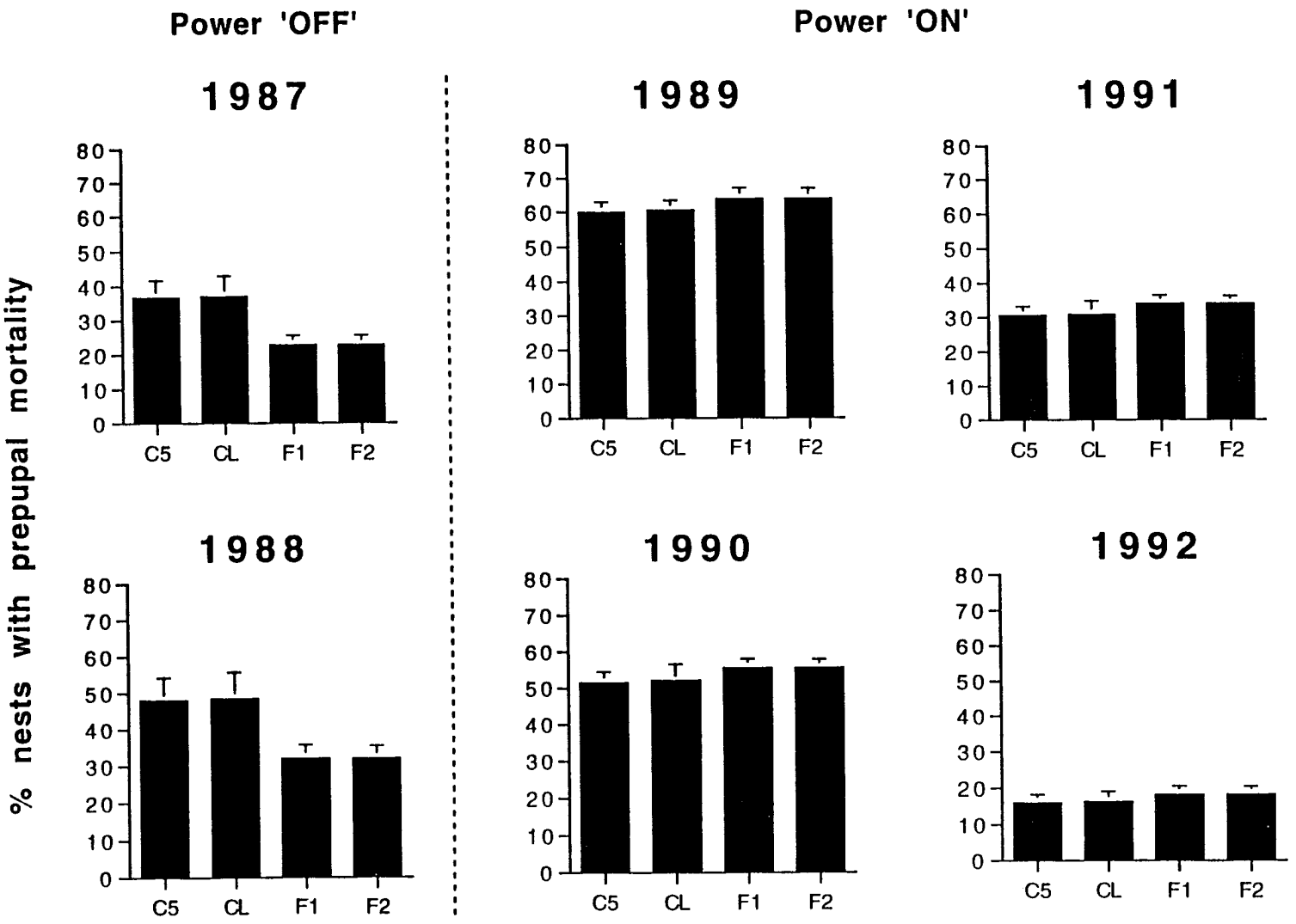


Figure 37a. Predicted percent of nests with prepupal mortality by year and site, *M. inermis*.

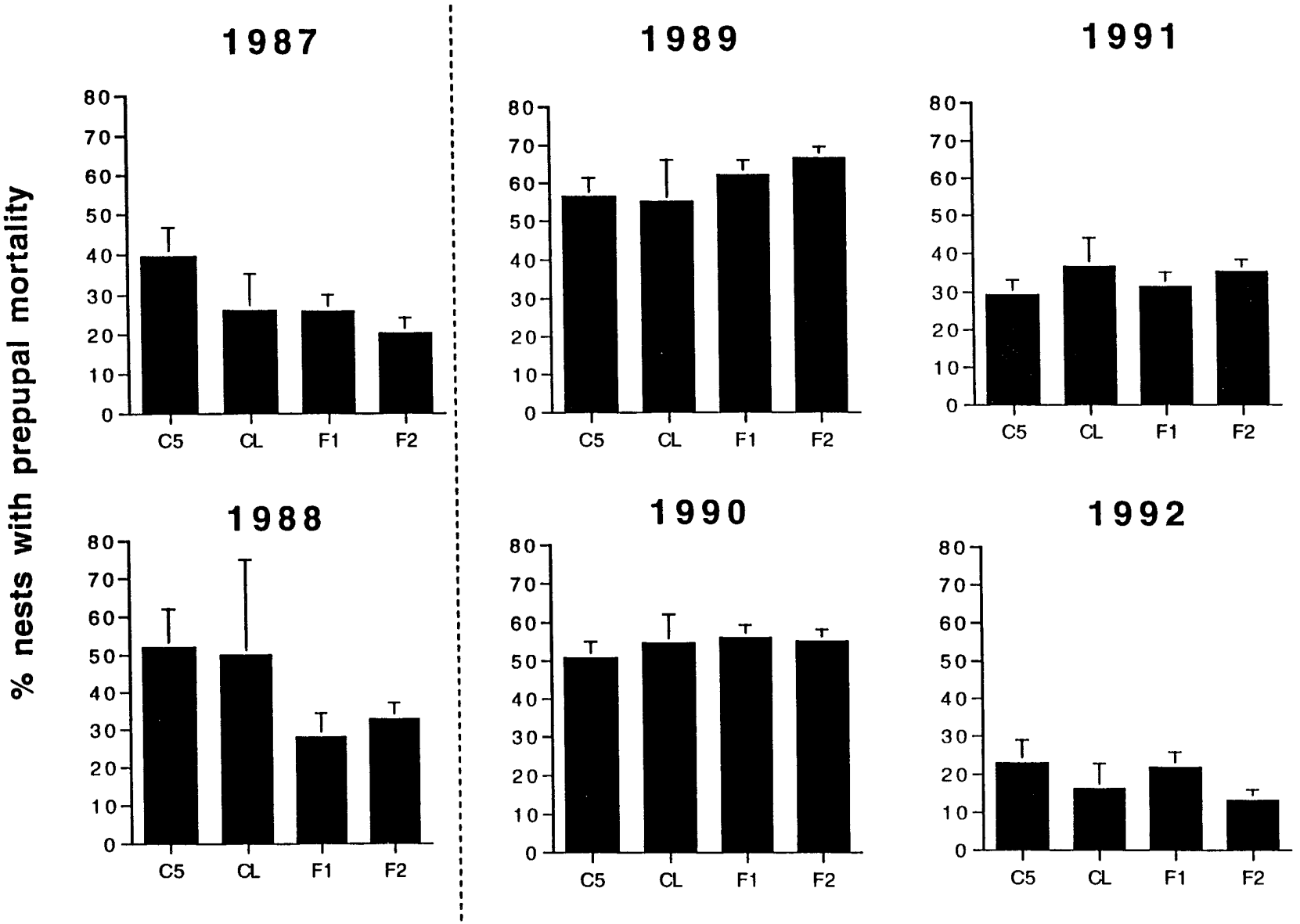


Figure 37b. Actual percent of nests with prepupal mortality by year and site, *M. inermis*.

TABLE 30. Categorical modeling analysis of nests with prepupal mortality vs. nests with pupae and adults for *M. inermis*, 1987 - 1992.

PROPORTION OF NESTS WITH PREPUPAL MORTALITY

Source of variation	df	Chi-Square	Prob.
Intercept	1	31.31	0.0000***
Exp	1	3.65	0.0560
Site [Exp]	2	0.01	0.9941
Antenna	1	2.78	0.0952
Year [Antenna]	4	197.46	0.0000**
Exp * Antenna	1	10.08	0.0015*
Residual	14	11.17	0.6723

Overwintering Mortality - *Megachile inermis*

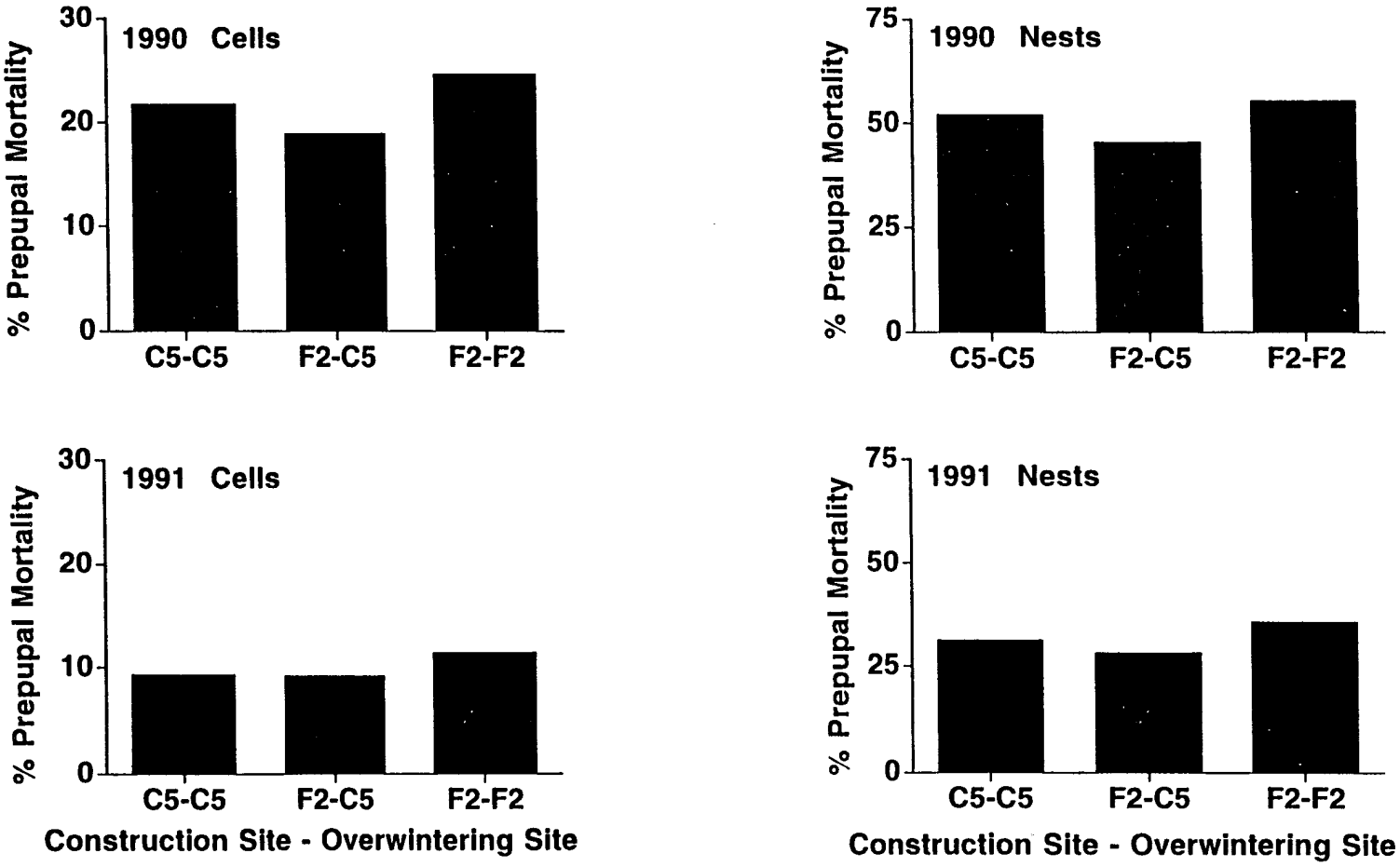


FIGURE 38. Percent prepupal mortality of 1990 and 1991 *M. inermis* constructed at the C5 or F2 site, and overwintered at the C5 or F2 site.

TABLE 31. Categorical modeling analysis of prepupal mortality of 1990 and 1991 *M. inermis* cells and nests constructed and overwintered at C5 or F2.

PREPUPAL MORTALITY OF *M. INERMIS* CELLS

Source of variation	df	Chi.Square	Prob.
Intercept	1	1355.93	0.0000***
Year	1	99.20	0.0000***
Overwintering site (C5 or F2)	1	6.64	0.0100*
Construction site [Ow site] (C5 or F2)	1	0.81	0.3669
Year * Ow Site	1	0.01	0.9247
Residual	1	0.35	0.5538

PREPUPAL MORTALITY OF *M. INERMIS* NESTS

Source of variation	df	Chi.Square	Prob.
Intercept	1	26.73	0.0000***
Year	1	35.10	0.0000***
Overwintering site (C5 or F2)	1	4.79	0.0286*
Construction site [Ow Site] (C5 or F2)	1	1.03	0.3093
Year * Ow Site	1	0.00	0.9927
Residual	1	0.16	0.6875

TABLE 32: Summary of parameters tested for ELF EM effects, and results.

SUMMARY OF SIGNIFICANT EFFECTS

Parameters tested	M. relativa	M. inermis	Detectible Differences	Comments on significant results
ELF EM fields may slow or disorient bees				
round leaf foraging time		ns	8-29% of mean	
Bees may reduce parental investment in offspring				
cell size	*	ns	3-9% of mean	control areas change
cells per nest	ns	ns	-1 cell per nest	
offspring sex ratio	ns		?	
offspring weight	ns	ns	10-30% of mean	
ELF EM fields may stress bees				
Bees may pad their cells				
nest plug length		ns	12-30% of mean	
leaves per cell	ns	*	2-15% of mean	differences greatest in low power years
Bees may change nest orientation			?	
C5	ns			
CL	ns			
F1	*			one of three hutch sets
F2	ns			
Overwintering mortality may increase				
Cells with prepupal mortality	n.s.	*	?	differences greatest in low power years
Nests with prepupal mortality	n.s.	*		